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PHYTOSOCIOLOGICAL STUDY OF SAN AUGUSTIN PLAINS, NEW MEXICO

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INTRODUCTION

The object of this study has been to map the distribution and to determine the composition of the principal vegetational types in the drainage basin of the San Augustin Plains. The results are reported here in a variety of phytosociological attributes along with a discussion of the influence of climate and soils.

One of the major deficiencies in the technique of determining past vegetation and climate by the pollen analysis of drill cores of various sedimentary materials has been the inability to translate pollen percentages of the profile into forest composition and a proper ecological interpretation of the species. This deficiency does not detract from the fact that a great deal has been learned on the basis of trends of indicator species and of the consistent repetition of the trends in different borings. Attempts to solve various aspects of the problem include studies of the pollen production of several species, the maximum distances of pollen transport, the rates of settling of air-borne pollen, the relative preservation in various sediments and the composition of pollen rain within a given forest type. Of primary importance in regional studies is a better knowledge of the distribution and composition of the vegetational types. Once this is known, correlations can be made with the current pollen rain produced by these types. The ideal topographic situation for this sort of study should be a large basin surrounded on all sides by successive altitudinal zones of vegetation.

The San Augustin Plains is a high elevation basin of an extinct lake surrounded by mountain ranges. Here is provided an excellent area in which to study the relation of pollen rain to vegetational types ranging from the shrubs of alkali flats to the moist mixed conifer forests of high altitudes. The drainage basin of the Plains includes an area of nearly 2,000 sq. mi. with an altitudinal range of about 3,000 ft.

One purpose of this study was to construct a map showing the location of the major plant associations which would be the principal sources of pollen carried into the basin. The distributional pattern of vegetation is an obvious prerequisite to determining distances of pollen transport. A second major purpose of this study was to determine the species composition of the several zones of vegetation. This information is prerequisite to later comparison with the species composition as represented in the current pollen rain, both within the zone of vegetation and at various distances from each zone. A third purpose was to express the ecological relationships of each zone in a number of ways, e.g. frequency, density, basal area, total coverage of foliage, and relative coverage. A fourth purpose was to recognize any ecological trends indicated by plant succession, such as those resulting from climatic changes.

Not only is the San Augustin Plains ideal for the study mentioned above, but there is an increasing fund of scientific knowledge accumulating on the history of this area to which a direct contribution can be made by an ecological study of the present vegetation and its relation to pollen rain. Following a study of Mexican basins started in 1948 by Sears and Clisby, the latter secured a 645-ft drill core from the basin of the San Augustin Plains in 1953. Under the general direction of Dr. Paul Sears of Yale University, an expanding investigational program has continued in the San Augustin Plains. The tectonic, volcanic, and erosional history of the area is being worked out from textural analyses, petrographic studies, and carbon dioxide determinations of the core by Dr. Fred Foreman of Oberlin College.

A study of the geomorphology of the Pelona Quadrangle at the southwest end of the Plains is being completed by Dr. Charles Stearns of Tufts College. Mrs. Kathryn Clisby of Oberlin College is completing the analysis of the drill core revealing dramatic changes in vegetational history and the indicated climate. A portion of this history has been reported by Clisby (1955) and Clisby & Sears (1956).

To the writer's knowledge, the only detailed vegetational studies which have been made of the San Augustin Plains drainage are the U.S. Forest Service timber management planning maps of the Apache and Gila National Forest Areas, the grazing type maps of the Forest Service and the Bureau of Land Management, and an unpublished study of Springfield (1951) on the effect of drought on the density and forage yield of a grassland study exclosure. Some general observations of plants in the area are made by Smith (1950) and by Clisby & Sears (1955).

To provide some fundamental information on present day pollen rain, a series of 8 stations was located across the drainage basin of the San Augustin Plains. Current pollen fall was obtained on greased glass slides for 24-hr, 7-day, and seasonal periods. The analysis of the pollen fall of the 1956 season will not be presented here. It will include a comparison of the distribution and composition of the present vegetation with the present-day pollen production and current pollen rain into various parts of the basin, distances of transport, and the relative preservation of pollen in surface soils of the playa or in moss and lichen polsters.

This study is a portion of a larger project on the San Augustin Plains under the general direction of Dr. Paul B. Sears of Yale University. The writer wishes to thank Mrs. Kathryn Clisby, Oberlin College and Dr. Sears for suggesting the study and for their guidance and support. The work was done during 1955-56, while on sabbatical leave from North Dakota Agricultural College, and was made possible through the financial assistance of a National Science Foundation grant. To the many staff and field members of the U.S. Forest Service Regional Office at Albuquerque, to Dr. E. F. Castetter of the University of New Mexico, and to Prof. Ross Moir I express my appreciation for their willing and helpful assistance. Also acknowledged are the friendship and cooperation of local ranchers which were essential to the success and pleasure of the field work.

General Characteristics

The San Augustin Plains is a high altitude, intermontane basin located along the eastern edge of the Continental Divide in west-central New Mexico. It is within the Colorado Plateau physiographic province in an area of nearly level volcanic rocks, which are often steeply eroded and which surround the basin as in the Basin-and-Range area to the west.

The major portion is in Catron County with only the northeastern end in Socorro County. The elongated basin has its long axis in a N.E.-S.W.direction with the plains area proper being about 54 mi. long. The width is variable from about 20 mi. at the northeast end to 6 mi. and less at the southwest end. Elevations within the plains vary from 6775 ft above sea level to about 6950 ft. The surrounding hills, mountain ranges, and peaks rise up to 3000 ft above the plains with maximum elevations at the southwest end of 9780 ft above sea level at Elk Mountain. The basin is bounded on the north by the mountains of the Gallinas and Datils; on the west by the hills of the Continental Divide, the Mangas and Tularosa Mountains; on the south by the Continental Divide formed by the Elk, O Bar O, and Pelona Mountains as well as the Luera Mountains; and on the east by the San Mateo Mountains. As shown on the map in Figure 1., the basin is located in ranges 6-16 West and townships 1 North-9 South from the New Mexico principal base line and meridian.

This study was arbitrarily limited to the watershed or drainage basin of the San Augustin Plains which is an area about 38 mi. wide and 72 mi. long.

The geological history of the area has best been described by Bryan (1926) and Powers (1939). The present plains area was about ⅗ filled by the extinct Lake San Augustin which attained a maximum elevation of 6940 ft above sea level during a former pluvial period. At this extent it was about 11 by 34 mi. in size, 255 sq. mi. in area, 165 ft above the present surface, and occupied about 13% of its drainage basin. This lake may be a part of the widespread Pleistocene lakes described by Meinzer (1922) although not included on his map. The San Augustin Plains basin is included, however, in a map of present and extinct pluvial lakes of the Basin and Range region by Dillon (1956).

In discussing the Pleistocene climate in New Mexico, Leopold (1951) states a belief that the lakes were contemporaneous with glaciers in the mountains. Antevs (1954) revised his previous dating of the last pluvial period which had been set to correspond to a late stage of the last deglaciation and due principally to heavy summer rains. His revised estimate is "that the glacial and pluvial culminations in the southwest were contemporaneous with each other and practically coexistent with those in the Great Basin and southern California." Also, he states that the pluvial period, with a maximum estimated at about 24,000 yrs ago, was caused by both lower temperatures and heavier precipitation, with snowfall of increasing importance southward. The lowering of temperature caused a lowering of life and climatic zones which he estimates to have been about 4,000 ft lower than at present at the latitude of Santa Fe, New Mexico. This would mean that the forests of the Canadian (spruce-fir) and Transition zones (ponderosa pine) may have covered the upper part at least of the Upper Sonoran zone (especially the pinyon-juniper). Antevs (1954) further states, "The plains and the basins of New Mexico were probably for the most part treeless then as now and for much the same reasons, namely, occasional severe droughts, unfavorable soils, poor drainage and aeration, strong winds, etc. However, most of the grass-

land may then have been, not short-grass steppe as today but tall-grass prairie . . . ."

In contradiction to the above, Sears & Clisby (1955) in a study of the Pleistocene climate in the tropical Mexico City area show that the moist periods of glacial advance were also relatively warm. This conclusion was derived from the pollen analysis of several drill cores. Accompanying the maxima of moist indicators (correlated with glacial advance) were a high percentage of warm temperature indicators, rather than cold temperature species.

Radiocarbon dates from the sediments of the San Augustin Plains indicate an age of 19700±1600 yrs at the 18-21.5 ft level of the 645 ft drill core. This dating indicates the slowness of deposition, at least within the zones of silt and clay accumulation, and gives an appreciation of the possible age of the entire core. One must acknowledge that layers of sand and gravel would represent shorter time intervals (Clisby 1955, Foreman 1956).

The existence of the lake is evidenced by the sediments, beaches, sand spits, and wave-cut cliffs which are present on all sides except the northeast. Today a low ridge of hills separates the large playa from the two small northern playas, White Lake and North Lake. Powers (1939) believes these hills to be alluvial fans plus sands which have been carried northeastward by lacustrine action and later by wind action from the dry lake basin. The recency of the lake is attested to by the fact that around most of the basin, the wave-cut shorelines cross alluvial fans, indicating the principal period of erosion to have been prior to the pluvial period. While examining aerial photos in the process of mapping the vegetative types, the writer observed many beachlines and sand spits. The position of these has been included on the vegetation map of this study. Powers also reports no evidence of faulting since the existence of the lake, while faulting has occurred in much of the Great Basin. However, the abrupt rise of the mountains on the southeast and northwest of the main playa suggested to Powers a fault origin of the San Augustin basin. This is apparently confirmed by unpublished maps of Stearns (1954) which show many fault lines in the southwest end of the basin. In a brief description of the geologic setting of the San Augustin Plains, Stearns (1956) describes the Plains as a "graben" where "in several marginal areas, minor faults parallel linear segments of the topographic margins of the basin. These faults would be appropriate secondary members of fault zones, the principal displacements in which form structural boundaries to the basin."

The lowest part of the basin is near the southwest end with an elevation of about 6775 ft. Within the 28 mi. from here to the northeastern edge of the former lake bed, the average rise in elevation is 5.7 ft per mi. The large playa, however, is very flat with a variation of only 5 ft in altitude over an area 7 by 5 mi. in size. The southeast and northwest shores rise sharply to the adjacent hills, where distinct beach ridges and wave-cut cliffs occur.

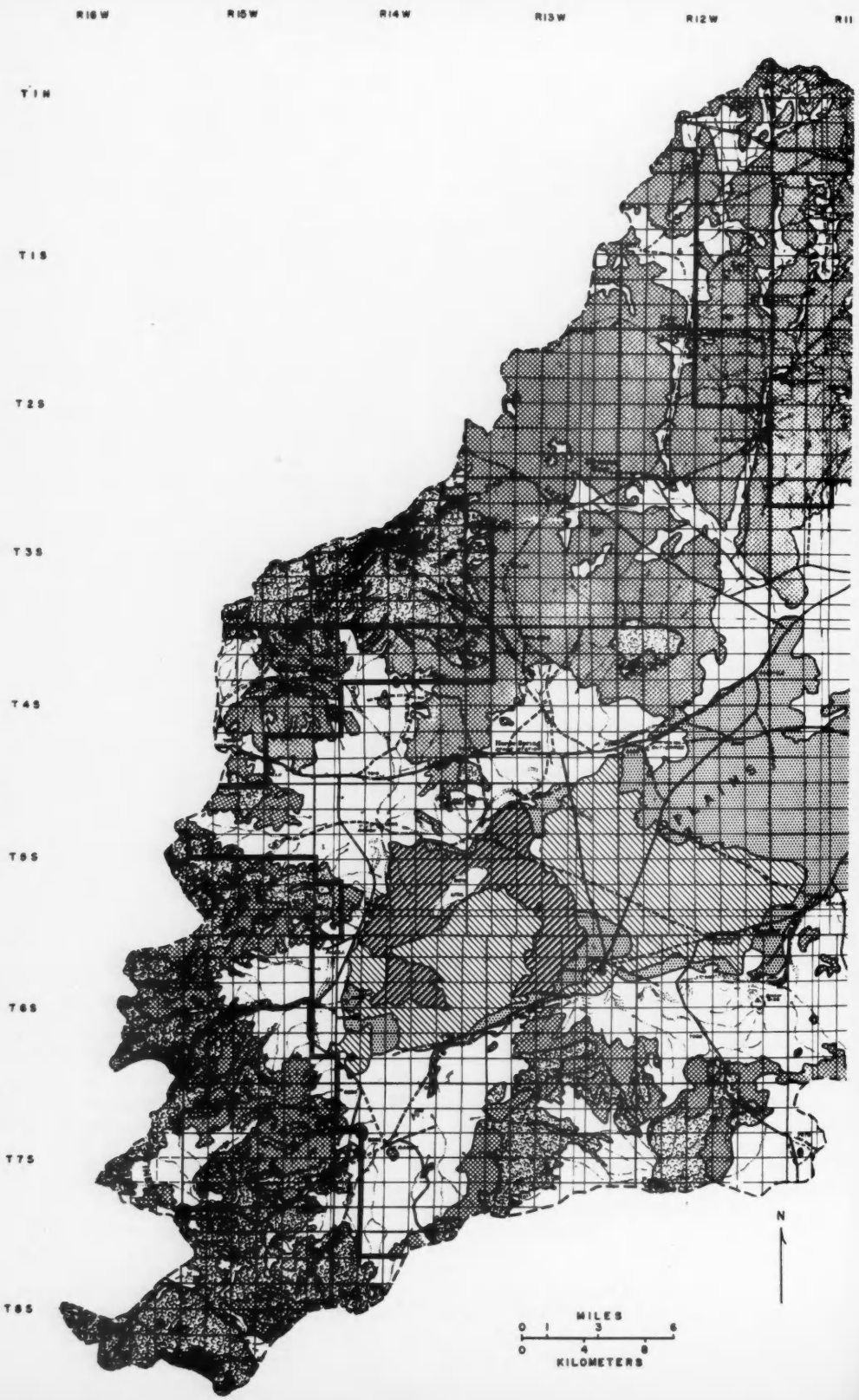
In the wave-cut cliffs of the southeast side, wave action cut out several caves from the softer layers of volcanic mud flow or ash material. The largest of these, Bat Cave, has been investigated for archeological materials including plant remains. Results have been reported by Mangelsdorf & Smith (1949) and by Smith (1950). In the latter publication, it was reported from radiocarbon dating of several strata that occupation probably occurred about 3500 yrs ago and as recently as 1752±250 yrs ago. Included in the plant remains were materials of hydrophytes requiring permanent bodies of shallow water, as well as evidence of Juglans and an abundance of acorns. In addition, there was evidence of cultivation of corn, beans, squash, and of the obvious need of a supply of drinking water—all of which would indicate a climate of higher precipitation and better seasonal distribution than existing today.

Stream action, important in the past, is of little consequence in the plains today. There is no inlet or outlet of the basin below 6925 ft elevation, so below this level there is interior drainage. Alluvial fans have been formed in the past at the mouths of canyons. During occasional flash rainstorms, ephemeral or intermittent streams flood out over the basin, depositing coarse volcanics, gravel, and sands on the alluvial fans and carrying finer silts and clays out over the basin. Usually the water disappears by seepage into the coarse substratum of the margins. The extra moisture received by flooding across the embayments produces the best grass stands of the area resulting in a contrast in growth of blue grama grass which forms a sharp line of demarcation at the edge of the flooded area. Across the silt and clay basin, water action is limited to small channels several inches to 1 or 2 ft deep with occasional, small, shallow pools where water may stand throughout the rainy season. In some areas following severe rain-storms, water from these channels disappears into deep cracks or underground chasms of apparently endless capacity. This action may well be related to the frequent "sinks" found in the silty area of the playa.

CLIMATE

The general region of the San Augustin Plains lies within the DD'd (semi-arid, microthermal, moisture deficient at all seasons) climatic zone, according to Thornthwaite (1931). The large, flat area of the plains at an altitude of 6800-7000 ft is characterized by a wide daily and annual range of temperature. The surrounding mountain ranges, which are 1-3000 ft higher, have slightly narrower temperature fluctuations.

The area is outside of the normal storm track so the precipitation is largely local and sporadic. July and August are the principal months of precipitation. Snowfall may occur from October to May, with the maximum amount in December. Some years the plains are barren of snow causing a serious deficit of moisture for spring growth. High winds and dust storms across the plains are common in spring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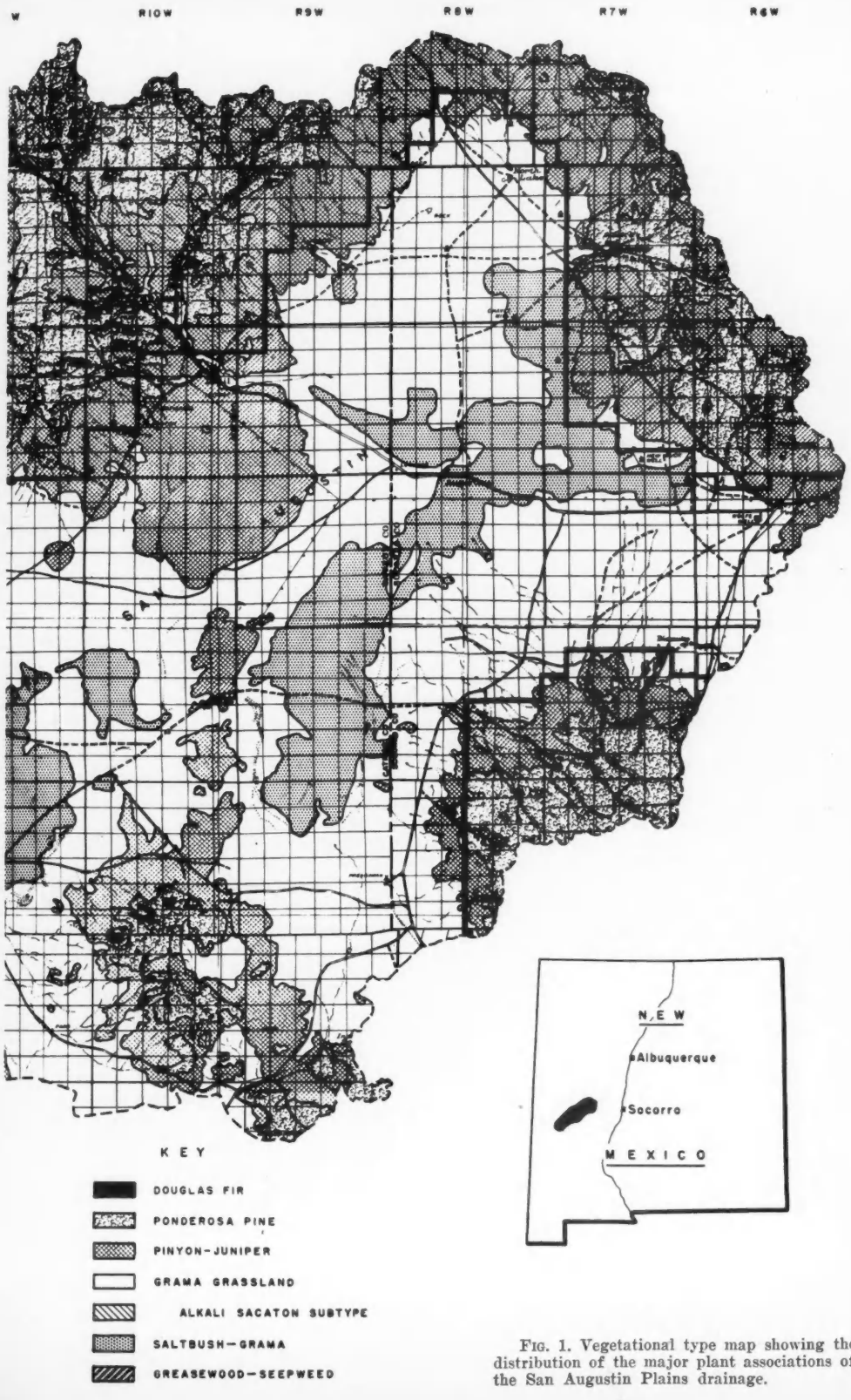

FIG. 1. Vegetational type map showing the distribution of the major plant associations of the San Augustin Plains drainage.

and early summer. Southwest winds are common to the majority of days for each month of the year. Sunshine occurs in about 70-80% of the days.

Climatic data are available from only 4 sites within the drainage of the San Augustin Plains. One of these, Horse Springs, is not currently reporting. The others have records of temperature and precipitation only. The only long-time record available is from Horse Springs at an altitude of 7070 ft on the north edge of the southwest end of the plains and in the pinyon-juniper woodland. Here the mean January temperature is 27.6°F, the July mean is 66.8°F and the annual mean is 47.6°F. Temperature extremes are −21°F and 105°F. The average frost-free period is from May 24 to October 1 (130 days), although frosts may occur any time from September to June inclusively. About 38% of the yearly precipitation is received during the warmest months of July and August. The annual precipitation is 13.32 in. (U.S.D.A. 1941 Yearbook of Agriculture). There is a short-period record of 11 yrs from the Birmingham Ranch, located at 6800 ft elevation in the grassland area. This site is about 11 mi. from Horse Springs. It shows a normal annual precipitation of 9.8 in., while a 17-yr normal at Augustine near the center of the grassland and toward the northeast end of the plains is 11.6 in. (U.S. Weather Bureau 1955). These latter two records show distinctly lower amounts of winter precipitation in the form of snow in recent years. This decrease in snow is substantiated by observation and comment of several ranchers in the area. The predominant wind direction for each month of the year is from the southwest (U.S. Weather Bureau 1932).

Although no data for evaporation are available, this factor is important and worthy of observation. In addition to high temperatures, sunshine, and frequent winds, the relative humidity is generally very low. Long periods of high evaporation stress place a large demand on the water-supplying capacity of vegetation, eliminating those perennials which do not have physiological or morphological drought resistance. Because the limited precipitation occurs largely as quickly passing summer showers with high temperatures and sunshine between, much of the rainfall is quickly lost from the surface soil by evaporation before it has an opportunity to infiltrate.

No weather records are available from the ponderosa pine zone. A general comparison of the climatic conditions in the three principal vegetative zones for the region is based upon Pearson's (1931) data for eastern Arizona and western New Mexico:

	Grassland	Pinyon-juniper	Ponderosa pine
Altitude (ft)	3700-5600	5100-7000	6500-8500
Mean annual temp.	56.3°F.	53.1°F.	47.7°F.
Annual precip.	11.36 in.	16.04 in.	21.61 in.

The maximum, minimum, and mean temperatures for June-September show differences corresponding closely to those of the annual period.

SOILS

Because the San Augustin Plains is not an important agricultural area, no soil surveys have been made. The area would be included in two general soil groups as follows: the plains area is in the Capulin-Tucumcari soils of the Brown Soils group, while the surrounding hills and mountains are in the McCammon-Deschutes soils of the Lithosol and Shallow Soils (arid-subhumid) (U.S.D.A. Yearbook 1938).

The Capulin-Tucumcari soils occupy grasslands of high plains and plateaus of New Mexico at 4000-7000 ft elevation. The parent materials are either sedimentary beds and their outwash, or sometimes basaltic in origin. Calcareous subsoils are general. In the San Augustin basin, texture varies from gravel beach ridges around the margin to the varying texture of alluvial material formed as outwash from the surrounding hills. These decrease from gravels up the embayments to the adobe clay in the center of the playas. As particle size decreases, porosity and infiltration decrease while alkalinity increases.

The McCammon-Deschutes soils are common to the juniper-covered ranges and high plateaus of the Great Basin and intermountain area. The parent material of the ranges surrounding the plains is entirely volcanic in origin and may be rhyolite, andracite, or basalt. The soils are usually shallow, stony, and on rough terrain. Surface soils, when present, are grayish-brown to dark brown. Many areas present an appearance often called "malpais," consisting of lava beds partly covered by a thin soil between thickly strewn fragments of lava.

In studying the tension zone between grama grass and pinyon-juniper associations in northeastern New Mexico, Emerson (1932) found that the usual rocky soils of the pinyon-juniper zone contained about four times as much available water at the 15-30 cm depth as in grasslands. The ground cover and the evaporation rates in the two zones were reported to be about the same.

Because of the apparent correlation of vegetation zones with relief and soils, a series of soil samples were obtained from the center of a barren area of the playa across three vegetation zones. The location of the transect was from the S.W. ¼ of Sec. 19, T5S, R13W in a north-northwest direction to the S. ½ of Sec. 12, T5S, R14W. Odd-numbered samples were from a depth of 0-3 in. as a composite of 5 samples. Even-numbered samples were composited from the 6-9 in. depth. Samples were obtained from the center of each vegetation zone and at about 15 ft above and below the transitions between types, which were very distinct in this area. The bare area of the playa extends over several sections and is completely devoid of vegetation. From a distance

it would appear that this area is the lowest part of the plains and at times would be covered with water, thus eliminating plant growth and acting as a basin for the accumulation of salts. This appearance is not entirely true at the present time, however. At the north end of the club-shaped area, with its long axis in a southwest-northeast direction, the silty clay soil is 3 to 5 ft higher than the surrounding area. This relief is not apparent at the southwestern end and may be the result of wind action from prevailing southwesterlies. Under the raised conditions with an encircling area of lower relief, it would appear that drainage would be improved in the bare area. The soil texture of the inner zones appeared similar and analysis showed them to be of silty clay. It was assumed that there was a difference in salt content, dominated by sodium and an accompanying high pH. Through the courtesy of Dr. Boyce Williams and the Soils Testing Lab of the New Mexico College of Agriculture and Mechanic Arts the analyses of Table 1 were obtained.

TABLE 1. Results of soil analyses of a transect across vegetative zones from bare soil of playa into surrounding grassland.

Site	No.	Depth	Texture	pH Paste	pH 1:5 (Dilutions)	% total Soluble salts
Bare area	1	0 - 3	Silty clay	8.5	9.4	.29
	2	6 - 9	" "	8.3	9.3	.40
Greasewood zone (*Sarcobatus vermiculatus*						
Inner margin	3	0 - 3	" "	8.5	9.4	.20
" "	4	6 - 9	" "	8.4	9.2	.43
Center	5	0 - 3	" "	8.3	9.0	.19
"	6	6 - 9	" "	8.2	8.9	.25
Outer margin	7	0 - 3	" "	8.2	8.8	.16
" "	8	6 - 9	" "	8.1	8.5	.36
Saltbush zone (*Atriplex canescens*)						
Inner margin	9	0 - 3	Silty clay loam	8.0	8.8	.12
" "	10	6 - 9	" " "	8.1	8.6	.25
Center	11	0 - 3	Silt loam	7.9	8.7	.14
"	12	6 - 9	" "	8.1	8.7	.21
Outer margin	13	0 - 3	" "	8.1	8.6	.07
" "	14	6 - 9	Silty clay loam	8.2	9.0	.11
Grassland zone (*Bouteloua gracilis*)						
Inner margin	15	0 - 3	Sandy loam	8.1	8.5	.02
" "	16	6 - 9	Loam	8.1	8.7	.08
Center	17	0 - 3	Sandy loam	8.1	8.2	.02
"	18	6 - 9	" "	8.1	8.4	.02

There is a general reduction of salt content and decrease of pH from the bare area outward. The two columns of pH determinations in Table 1 represent electrode analyses with two dilutions of water. Paste represents a dilution of soil with about equal parts of water and the 1:5 with five times as much water. Large differences in the two determinations generally indicate sodium content. That there is essentially no difference between samples 1-2 and 3-4 is not surprising, as the latter were taken from the sloping edge of the raised bare area. Samples 1-6, and 8, 10, and 12 would be considered saline-alkali (sodium) soils. The salt and sodium content of samples through the saltbush zone would affect plant growth to some extent. The coarser sandy loam soils of the grassland are relatively free of both salts and sodium. It is also apparent that infiltration and aeration would increase from a low level in the bare area to the soils of the grassland, because of a decrease in salt content and finer textures. Pools of standing water due to sealing of surface layers are common in the greasewood area, while uncommon or non-existent in saltbush and grassland. Almost universally the soils supporting saltbush show evidence of drifting due to wind action, scouring out between plants, and accumulating around the base of bushes. Grassland soils are on increasing degrees of slope and show the effect of water erosion by a surface of large particles in the manner of desert pavement.

METHODS OF VEGETATIONAL ANALYSES

VEGETATIONAL TYPE MAP

The vegetational types within the drainage of the San Augustin Plains were mapped from stereo pairs of aerial photos at a scale of 1:40,000. The following types were delimited:

Greasewood-seepweed
Saltbush-grama
Grama grassland with Alkali sacaton as a subtype
Pinyon-juniper (foliage cover of 10% or more of pinyon, juniper and oak)
Ponderosa pine (where species comprises 50% or more by gross volume of conifer saw timber)
Douglas fir (mixtures of commercial conifer species not conforming to above types, dominated by Douglas fir)

The brush types in some areas were indistinguishable in the aerial photos, although the identification of the sites of greasewood and seepweed was sometimes possible from the soil character. These plants are largely limited to the large playa, where the soils are silty clay, which is distinguishable from the air by its light color and the pattern of cracks, some of which are permanent features. The boundaries of these types were checked by ground reconnaisance and triangulation from known points. Timbered types were also ground-checked where there was any doubt of the composition. Most areas were not classified below a minimum size of about 40 A. Thus areas having a variety of slope exposures may be classified as one type but have small patches of another type mixed in, e.g. patches of juniper on southwest exposures in a ponderosa pine type, or narrow strips of ponderosa pine in valleys of a juniper type.

The locations of beach lines and sand bars which were discernible on the aerial photos were also included on the overlays.

After the types on the overlays were checked, the type boundaries were transferred to aerial planimetric quadrangle maps at a scale of 2 in. per mi. by the use of a K.E.K. Plotter. These maps were then reduced by photographic reproduction. The essential lines and data were redrafted (the types distinguished by the use of Zip-a-tone), and the map photographically reduced again to the final scale. The process of doing the initial work on large sized maps was not only most expedient because of the size of the accurate planimetric maps available, but also provided greater accuracy in the reduced scale of the final map. The area occupied by each vegetative type was determined by the use of a planimeter.

HERB AND SEEDLING STRATUM

The vegetation of the drainage basin of the San Augustin Plains was divided into five associations: (1) Ponderosa pine *(Pinus ponderosa)*, (2) Pinyon-juniper *(Pinus edulis-Juniperus)*, (3) Grama grassland *(Bouteloua gracilis)*, (4) Saltbush-grama *(Atriplex canescens-Bouteloua gracilis)*, and (5) Greasewood-seepweed *(Sarcobatus vermiculatus-Suaeda suffrutescens)*. The terminology of grasses follows that of Hitchcock (1950), for other species, that of Kearney & Peebles (1951). Each association was represented by 10 stations which were distributed throughout the area of the type and were selected as being typical of the vegatation of that area of the basin. This sampling technique did not apply to the forest types which will be discussed later. Stands for analysis were chosen on the basis of their homogeneity of physiognomy, composition of apparent dominants, and by the typicalness of the site. Stands excessively disturbed by severe overgrazing and erosion were not used and marginal areas were avoided.

The purpose of the study was to obtain as representative a picture of the dominants of the entire region as possible. The great extent of the area involved seemed to necessitate a survey type of sampling with numerous stations, widely dispersed, and with widely spaced samples at each station to include as many of the local variations as possible. A one-square foot wire quadrat frame with an upright handle was used as a sampling unit. Quadrats of about this size have given satisfactory results under several similar circumstances (Voigt & Weaver 1951, Rice & Penfound 1954, Kelting 1954). Twenty-five samples were taken at intervals of 15 steps (37.5 ft) along each side of a square, the sides of which were aligned in a north-south and east-west direction. Thus, 100 quadrats were dispersed along a total linear distance of 0.7 mi. By sampling 10 stands in each type, a total of 1000 quadrats was used on which frequency and relative coverage were based. The large linear distance of this series of quadrats often revealed variations which would have been overlooked with a more compact system of sampling. These variations may not be of statistical importance, but observation of them was of value to the writer in appreciating such features as aggregation, sociability, site variations, and various biotic influences.

For each quadrat the following information was recorded: (1) percentage of total herbage coverage. These studies were made in October and November when full herbage growth had been attained, following the growing season aided by the July and August rains. Percentage coverage was estimated to the nearest 5%. (2) Each species was listed and classified into groups 1-5 (0-20%, 21-40%, etc.) on the basis of relative coverage of the vegetation present.

It should be noted that the existence of any vegetation in a quadrat resulted in a coverage value for that quadrat of at least 5% and for any single species a relative coverage class of at least 1.

The herb and seedling stratum was studied by this method in all except the ponderosa pine association during October and November of 1955. The ponderosa pine association was sampled in June and July of 1956 at the same time as the study of the forest tree composition was being made.

The quadrat data for the herb and seedling stratum were analyzed and expressed as the following attributes for each type in Tables 2,3,4,7, and 10:

(1) The herbage cover of all species except trees in each type, or those plants over 3 ft high in the woodland and forest types, is expressed as the maximum, minimum and also as the mean herbage cover of all stands representing the vegetative type.

(2) The frequency of vegetated quadrats (100 per stand) is given as maximum, minimum, and mean of the stands.

(3) The number of species per stand sample is also expressed as the maximum, minimum, and mean of the stands, as well as the total in all stands.

(4) Mean herbage cover when the species was present serves as a measure of local abundance, i.e. a species low in mean herbage cover but with a high frequency would be of high density and/or high relative herbage cover. Or, a species may be high in mean herbage cover when present but low in frequency, thus indicating dense, but scattered, clumps.

(5) From the observed data, the best single expression is that of relative herbage cover of the entire type which is occupied by each species. This was obtained by dividing the sum of all the coverage classifications for each species by the total coverage classifications of all species and expressed as a percent. The species are arranged for each type according to their decreasing importance on this basis.

(6) The frequency index for each species per vegetational type is given.

(7) Relative frequency is a comparative rating of distribution obtained by dividing the total of frequencies for all species into the frequency index of each species times 100.

(8) Constancy represents the percent occurrence of the species among the stands sampled.

MATURE TREE AND THE SAPLING AND BRUSH STRATA

In the phytosociological study of the pinyon-juniper woodland and ponderosa pine forest, the general method of sampling and analysis follows that of the line-strip method as described by Woodin & Lindsey

(1954) and further tested and modified by Lindsey (1955).

The forested area which was of particular interest in relation to composition and pollen production was that area surrounding the southwest end of the San Augustin basin. Because of prevailing southwesterly winds this area is the principal source of pollen blown into the basin where the current pollen rain was determined. Therefore, 10 sampling sites in each type were located by randomization along equally spaced radiating lines in a semi-circle lying to the southwest of the site of the drill core used for palynological study, Clisby (1955), and the pollen traps of the basin used to check present pollen fall. From observation of the forests surrounding the plains, the southwestern forests do not appear to be unlike the rest of the area in form or general composition. It is suggested that, in general, they would typify the forests surrounding the San Augustin Plains.

Random numbers were used to represent distance in miles from the drill core site along the radiating lines. The first number to fall within each of the two forest types as delimited on the vegetation cover map for the area was used as the area of sampling. This point was then transferred to the transparent overlay on the appropriate aerial photo. Three strips bent in the middle at a right angle in the form of an "elb" were used at each sampling site. Because of the irregularities in topography and resulting habitats, it was felt this shape of line-strip would sample the area more satisfactorily than a straight line. The same thought applied in the alignment of quadrats in the form of a square (a double elb) in sampling the non-forested areas.

Working in the pinyon-juniper type farther east of the Continental Divide, Woodin & Lindsey (1954) found that 7 line-strips provided information for cover and density of the important species with standard errors of less than 20% of the mean. They reported an average error of 12.5% for *Pinus edulis* cover and 9.9% for *Juniperus monosperma*. Percent errors for numerical abundance closely paralleled those for cover. For species with very low cover and density it is impossible to attain low percent errors with a reasonable number of sampling units. In this study is was felt that a better representation of the two types in the area would be obtained by a large number of sampling sites dispersed over the area. As the work proceeded, the visible variations in sites further substantiated the need of a large number of dispersed sampling sites of fewer elbs rather than a larger number in limited areas. Each vegetative type in this study is represented by 30 elbs.

The 3 elbs per site were nested in 3 directions from the sampling point. The line for foliage interception was established with a 100-ft steel tape, which was moved 4 times for each arm of the elb. The 20-ft strip, 10 ft on either side of the intercept line, was maintained without establishing outer lines. When a tree trunk was questionably close to the border of the strip, its distance from the line was checked by twice laying out a 5-ft sighting stick.

Working along the tape line, records were made of all species having foliage interception over the line if the plants were 3 ft high or more, the nearest foot unit of the tape below the near edge of the foliage, the nearest foot unit below the far edge of the foliage, and the stem diameter of the tree if it was within the 20-ft strip and 4 in. or more in diameter, or of equivalent basal area. The line interception data were recorded on the left side of the field sheet for individuals with stem diameters of 4 in. or more and on the right side of the sheet for individuals with stems of less than 4 in. diameter. Diameters were also determined for all non-intercept trees having stems in the 20-ft strip and with stem diameters of 4 in. or more. Diameters were estimated or measured with a d.b.h. tape to the nearest inch. The diameters of ponderosa pine were measured at the customary breast height (4.5 ft), while those of junipers, oaks, and pinyon were measured at 1 ft above the ground because of their habit of low branching. Where branching was below the 1-ft level, the diameters of the several stems were recorded and later converted to total basal area in square feet. Only those trees having a total stem basal area equivalent to that of a single 4-in. stem or larger were used for analyses in the mature tree stratum. If less, they were included in the sapling or brush stratum. All trees were grouped into 50-ft units along the entire length of the tape. These areas of 50 x 20 ft are considered as separate strip quadrats for the analysis of frequency. This area amounts to 1000 sq. ft, which is very close to the area of the commonly used $10m^2$ quadrat (1089 sq ft) and could be compared to studies using the latter unit. Unless it is desired to calculate a dispersion index for each species, it is not necessary to measure the position of each tree along the line, except to place it into the proper 50-ft unit.

All trees and shrubs 3 ft or more high but with stem diameters less than 4 in. were counted by species and also recorded in units of 50 x 20 ft in a separate column on the field data sheet. This information was used in the determination of frequency and density for species in the sapling and brush stratum.

As in the study of the vegetation of the lower zones of the San Augustin Plains, 100 quadrats, each 1-ft square, were employed in each of the 10 sampling sites. In each quadrat the total foliage cover was estimated to the nearest 5%, and the species were grouped into 5 classes (1-5) of relative foliage cover (1-20%, 21-40%, etc.). These quadrat samples were obtained in traversing the distance from one elb to another. This sampling resulted in 33 quadrats for each of the elbs, a total of 100 quadrats per site, and 1000 quadrats for each vegetational type. All plants less than 3 ft high were included in the quadrats. Thus a measure of all size groups was obtained.

The above field information was used to determine the following vegetational attributes for the three strata: Mature trees (stem diameters of 4 in. or more), saplings and brush (trees and shrubs 3 ft

or more high but with stem diameters less than 4 in.), herbs and woody seedlings.

Mature tree stratum.—Foliage cover, including relative foliage cover, percent ground cover, square feet of cover per acre, and mean crown diameter, was based on the line interception whether the stems were in the strip or not. Relative foliage cover = 100 × footage of line intercept per species on all lines/total footage of line intercept for all species on all lines. Percent ground cover = 100 × footage of line intercept per species on all lines/total length of all lines. Square feet of cover per acre = Relative foliage cover × 43560. Mean crown diameter $= 2\sqrt{\frac{\%\text{ ground cover} \times 43560}{3.1416 \times \text{density per A.}}}$

Density, both as relative density and as density per acre, was based on the total counts of mature trees having stems within the strips. Relative density =100× number of individuals of a species in all quadrats/total number of individuals of all species in all quadrats. Density per acre = 43560 × number of individuals of a species in all plots/square foot area of all quadrats.

Basal area, both as relative basal area and as square feet per acre was based on stem diameters. Relative basal area = 100 × total basal area of a species in all quadrats/total basal area of all species in all quadrats. Square feet of basal area per acre = total basal area of a species in all quadrats × square feet area of all quadrats/43560.

Frequency, both normal frequency index and relative frequency, was based on the 50 x 20 ft strip quadrats, of which there were 16 per elb, 48 per sampling site, and 480 for the entire type represented by 30 elbs at 10 sampling sites. Frequency index = 100 × number of quadrats in which the species occurs/total number of quadrats. Relative frequency = 100 × frequency index/total of frequency indices for all species.

Sapling and brush stratum.—Foliage cover, including relative foliage cover, per cent ground cover, and square feet per acre was based on the line interception of this class of plants.

Density, both as relative density and as density per acre, was based on the total counts of this class within the strips.

Frequency, both normal frequency index and relative frequency, was based on the 50 x 20 ft strip quadrats.

Herbaceous and seedling stratum.—The attributes were expressed like those of the non-forested areas.

RESULTS AND DISCUSSION

Distribution of Vegetational Types

The analyses of this study indicate that the several vegetational types delimited on the map, Fig. 1, would be physiognomically classified and interpreted by strata by Kuchler's (1949, 1955) method as follows:

Douglas fir forest—EmcDspHlp
- Evergreen needleleaf trees, 10-25m tall, continuous growth
- Deciduous broadleaf shrubs, scattered
- Forb herbaceous layer, low scattered patches.

Ponderosa pine forest—EmiDspGlp
- Evergreen needleleaf trees, 10-25m tall, not touching
- Deciduous broadleaf shrubs, scattered
- Graminoid herbaceous layer, low, scattered patches.

Pinyon-juniper woodland—EliDsrGlp
- Evergreen needleleaf trees, low, not touching
- Deciduous broadleaf shrubs, rare
- Graminoid herbaceous layer, low, scattered patches.

Grama grassland—Glc
- Graminoid, low, continuous

Saltbush-grama shrub—DzpGlp
- Deciduous broadleaf dwarf shrubs, scattered
- Graminoid herbaceous layer, low, scattered patches.

Greasewood-seepweed shrub—DszpGlr
- Deciduous broadleaf shrub, scattered
- Deciduous broadleaf, dwarf shrub, scattered
- Graminoid herbaceous layer, low, rare.

The total area of the drainage basin of the San Augustin Plains has been calculated to be 1,262,952 A., or 1,937 sq. mi. According to the measurements obtained by the use of a planimeter and the vegetative type map of Figure 1, the drainage basin is divided into the following vegetational type areas and percentages:

Vegetational type	*Acreage*	*Percent*
Grama grassland	527,043	41.7
(alkali sacaton subtype)	(49,252)	(3.9)
Pinyon-juniper woodland	397,913	31.5
Ponderosa pine forest	199,346	15.8
Saltbush-grama	117,078	9.3
Greasewood-seepweed	20,452	1.6
Douglas fir forest	1,120	0.9
Total	1,262,952	100

The grassland with or without the inclusion of the alkali sacaton subtype, occupies the greatest area of any type. It is found as a relatively broad zone below the pinyon-juniper woodland. It is also found in broad valleys and across ridge tops within several vegetational types. Alkali sacaton, as a subtype of the grama grassland, occupies several large regions near the Southwest end of the basin. Alkali sacaton is characteristic on soils which are finer in texture and lower in alkalinity than those of the saltbush-grama type. On the other hand, alkali sacaton is the dominant on soils which are coarser in texture and less alkaline than those supporting the greasewood-seepweed type. The sacaton and greasewood types are limited to the low-elevation areas of the basin. The area of grassland is followed closely by that of pinyon-juniper, which in turn is twice as

extensive as the ponderosa pine forest. The saltbush-grama type occupies extensive areas of sandy soil throughout the length of the Plains. The greasewood-seepweed type occurs in a crescent-shaped area which is practically uninterrupted by any other vegetative type. Within this type, the soils reach their finest texture and greatest alkalinity and the vegetation reaches its greatest sparsity. In fact, an area of about 1.5 sq. mi. within this type is barren of vegetation.

Greasewood-seepweed Association

This type shows wide variation in foliage cover from a maximum where greasewood *(Sarcobatus vermiculatus)* forms a dense stand of tall shrubs with its codominant seepweed *(Suaeda suffrutescens)*, to areas with only a few scattered plants of either one or the other species occurring alone in the center of the playa. The two extremes of this type are illustrated in Fig. 2 and Fig. 3. Greasewood is generally recognized as an indicator of alkalinity and high water table. The species is found in the lower part of the playa with seepage water highly charged with alkali salts and located not far below the surface. The surface soils often exceed a pH of 9.

Fig. 2. Barren area of playa with scattered plants of Sarcobatus and Suaeda. Note the texture of the silty clay soil and the cracking.

Fig. 3. Dense stand of greasewood *(Sarcobatus vermiculatus)* up to 7 ft tall. Understory of seepweed *(Suaeda suffrutescens)* and patches of alkali sacaton *(Sporobolus airoides)*.

Seepweed is commonly found around the base of the shrubby greasewood plants, or extending out into the barren flats along the margins of large cracks of drainage channels in the silty clay. Here seepweed occurs alone or with alkali sacaton *(Sporobolus airoides)*. An annual species of seepweed *(Suaeda diffusa)* is also common on the alkaline flats.

The number of species which can endure the alkaline, adobe clay is very few as indicated by the low mean of 5 species per stand (Table 2). The soil conditions in the central area of the playa are extreme. Relief is practically nil and the water table is only a few feet below the surface. Water stands over the lowest part of the area for short periods during some years. During periods of high moisture the clay swells with water of imbibition and absorption at the expense of the air space. The surface becomes sealed off to gas exchange. With drying, shrinkage occurs and cracks develop across the surface. All stages in this process can be observed around the small pools of surface water. The entire basin exhibits similar features of cracking on a larger scale as seen in aerial photos, Fig. 4.

Table 2. Ground cover of herbs and shrubs in the Greasewood-seepweed zone based on 1000 1-sq. ft. quadrats.

Species	Cover		Frequency		Constance
	mean herb cover when present (0-5)	rel. herb cover %	freq. index %	rel. freq. %	%
Sarcobatus vermiculatus	4.3	33.0	15	30.4	80
Suaeda suffrutescens	4.3	31.8	14	28.6	80
Sporobolus airoides	3.4	14.8	8	16.1	70
Suaeda depressa	4.0	3.9	2	3.3	20
Atriplex canescens	4.1	3.3	2	3.0	10
Salsola kali	2.3	3.2	2	4.4	30
Chenopodium album	3.1	3.1	2	3.6	40
Bouteloua simplex	2.8	2.6	2	3.6	10
Amaranthus sp.	3.4	1.3	1	1.4	20
Muhlenbergia wrightii	2.7	1.0	1	1.4	10

Summary of 10 sites (1000 quadrats)	Max.	Min.	Aver.	Total
Foliage cover (%)	24	0.2	7	..
Frequency of vegetated quadrats (%)	76	2	35	..
Total species per site	12	1	5	17

Species with less than 1% relative herbage cover: *Muhlenbergia wrightii, Bouteloua gracilis, Aster arenosus, Aristida divaricata, Munroa squarrosa, Salvia subincisa, Sporobolus minutissima.*

The view in this figure shows an area of 9 sq. mi. of the playa illustrating an unusual feature of surface relief not visible from the ground. The central area is located on Sec. 32 and 33 of T5S, R 13 W. The area around the margin represents the cracking into a polygon pattern typical of this area and of sub-arctic and arctic soils. In northern areas the pattern is caused by frost action. The central area of the photo, however, shows a contrasting pattern of cracks which are at right angles to each other. The northeast direction (marked by the arrow). This direction of one set of cracks corresponds to the longitudinal axis of the basin in a general southwest-orientation would suggest some relationship between

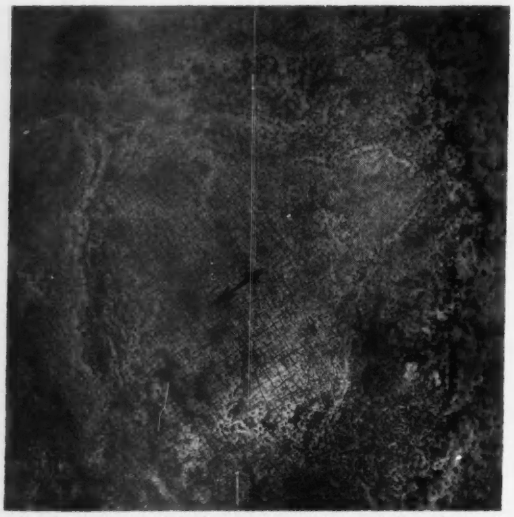

FIG. 4. An aerial photo of a section of the playa at the southwest end of the San Augustin Plains showing the pattern of soil cracking. Note the cracks in the central area at right angles to each other and aligned with the axis of the plains basin (indicated by the arrow) in contrast to the typical polygon areas of the margins.

the pattern of cracking and either the pattern of deposit of the clay into the basin or the physical effects of the contour of the basin. The large cracks shown in aerial view are often 1-3 ft wide, equally deep, and rather permanent. It appears that they were at one time much deeper and have become partially filled in. Long-time residents of the area report that during years of high rainfall there is an active development of these cracks and of slump areas which become dangerous as pitfalls for livestock. Moisture is retained in the cracks after the soil of the general surface level has become dry. At the same time, aeration of the margins may be better than in the adjacent flats. Rows of vegetation develop along the margins of the cracks, consisting principally of greasewood, seepweed, and alkali sacaton (Fig. 5).

FIG. 5. Vegetated playa cracks, here principally seepweed and alkali sacaton. Note the relative vigor of vegetation along the cracks and the dead or near-dead sacaton clumps in the foreground.

Near the margins of the playa the soil below the surface crust may be sandy, while nearer the center, the subsurface soil is very fine and of a crumbly, honey-combed nature.

In areas where grazing had been light for several years, there was a noticeable increase in the density of seepweed, but little increase in the density or vigor of alkali sacaton. The type is of very low grazing value for cattle except for winter grazing on the patches of alkali sacaton, Aparejo grass *(Muhlenbergia utilis)*, and saltgrass *(Distichlis stricta)*. The type is also used for wintering of sheep and for spring lambing grounds.

SALTBUSH-GRAMA ASSOCIATION

Patches of this type partially circumvent the large playa at the southwest end of the basin where it forms a transition from the inner, shrubby greasewood to the bordering grama grassland. In a few places there is a strip of alkali sacaton between the greasewood and the saltbush. The soils are less alkaline, of coarser texture, better drained and with little or no evidence of standing surface water. The effect of the heavy alkaline soil of the inner edge of the zone is indicated by one sampling site which was located near the margin and supported only 3 species. Here, the large patches of alkali sacaton made it the dominant cover, followed by four-winged saltbush or "chamisa" *(Atriplex canescens)* and seepweed. Farther out, patches of Aparejo grass and spike muhly *(Muhlenbergia wrightii)* become important. As the elevation increases, coarseness of the soil texture is indicated by an increase in blue grama grass *(Bouteloua gracilis)* and sand dropseed *(Sporobolus cryptandrus)*. The nearly ubiquitous Russian thistle *(Salsola kali)* reaches its greatest importance in this type, being second to blue grama in herbage coverage, Table 3. A general view of the type and its dominant shrub, four-winged saltbush, is shown in Fig. 6. Saltbush is not found in the heavy clay soils of the playa flat but on soils of intermediate alkalinity and texture. Where water storage reservoirs are constructed of earth and the diggings are piled up permitting improved drainage and decreased alkalinity, but providing a favorable water supply from below, four-winged saltbush invades the mounds. The concentration of saltbush on these disturbed sites is often very high in contrast to that of surrounding flats where it may be of little importance.

In addition to its distribution around the playa, the type extends northeastward in intermittent stands up the middle part of the old lake basin and on the sandy soils, which Powers (1939) believed to be windblown from the dried lake bed. The area is of low relief, blow-out and dune topography with evidence of present as well as past wind activity. Much of the area has been heavily grazed. Thirteen species of the total of 30 for the entire type are restricted to stands having sandy soils capable of blowing. Prominent among these are *Descurainia obtusa, Acanthochiton Wrightii, Bouteloua simplex, Zinnia grandiflora,* and *Ambrosia artemisiifolia*. These sites are also the

TABLE 3. Ground cover of herbs and shrubs in the saltbush-grama zone based on 1000 1-sq. ft. quadrats.

Species	Cover		Frequency		Constance
	mean herb cover when present (0-5)	rel. herb cover %	freq. index %	rel. freq. %	%
Bouteloua gracilis	3.4	25.7	41	19.8	80
Salsola kali	2.4	22.5	46	22.3	80
Sporobolus airoides	4.4	9.3	11	5.3	30
Sporobolus cryptandrus	2.7	7.6	15	7.3	60
Atriplex canescens	2.9	7.5	14	6.7	100
Aster arenosus	1.4	6.3	20	9.8	70
Munroa squarrosa	1.6	5.4	20	9.5	80
Sporobolus contractus	3.0	4.8	8	3.9	40
Descurainia obtusa	2.4	2.6	6	3.1	30
Aristida adscensionis	1.3	2.0	7	0.7	40
Sphaeralcea spp.	1.8	1.2	5	2.2	40
Suaeda suffrutescens	4.7	1.2	1	.7	20

Summary of 10 sites (1000 quadrats)	Max.	Min.	Aver.	Total
Foliage cover (%)	28	11	18	....
Frequency of vegetated quadrats (%)	100	58	89	....
Total species per site	16	3	9	30+

Species with less than 1% relative herbage cover: *Acanthochiton wrightii, Bouteloua simplex, Zinnia grandiflora, Muhlenbergia torreyi, M. utilis, M. wrightii, Ambrosia artemisiifolia, Chenopodium album, Euphorbia* sp., *Chrysothamnus* sp., *Amaranthus* sp., *Androsace septentrionalis, Aristida divaricata, Dithyrea wislizeni, Gilia longiflora, Gutierrezia lucida, Psoralea tenuifolia,* Misc. sp. unidentified.

FIG. 6. Saltbush type dominated by four-winged saltbush *(Atriplex canescens)*. Characteristic sandy soil capable of blowing is illustrated. Sand dropseed *(Sporobolus cryptandrus)* is the dominant understory on such sites.

ones having the highest number of species per stand.

Four-winged saltbush provides a valuable forage for both cattle and sheep and when mixed with alkali sacaton provides excellent winter range, being more valuable in mixture than either species alone. Large areas which were heavily grazed during drought years, however, now show reduced vigor and often complete death.

GRAMA GRASSLAND ASSOCIATION

This type covers the greatest area of the San Augustin Plains, extending from the outer edges of the saltbush-grama or the greasewood-seepweed associations up the gentle slopes and into the bordering

FIG. 7. Gentle slopes of plains margin of predominantly blue grama grass on well-drained soils of coarse texture.

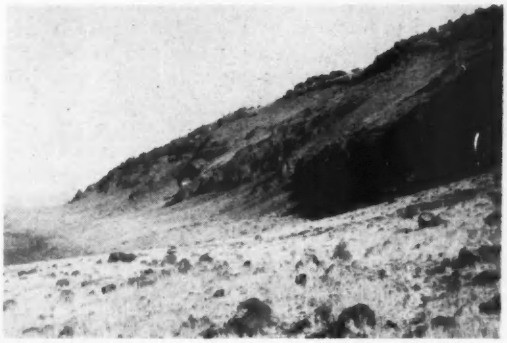

FIG. 8. Rocky, Volcanic Wave-cut cliffs near Bat Cave. The widest variety of grasses is found in varying microhabits. Note the saltbush basin on the left and the pinyon-juniper on the upper slopes at the right.

hills and mountain bases. These two situations are illustrated in Fig. 7 and Fig. 8.

Although the San Augustin Plains are as far south as some areas occupied by desert plains grassland, the altitude is high enough to provide more mesic conditions. The vegetation fits neither the *Bouteloua eriopoda-Hilaria mutica-Bouteloua rothrockii* faciation nor the *Hilaria belangeri-Bouteloua gracilis* faciation of Whitfield & Beutner (1938). Nor does one find representatives of the typical desert grassland shrubs, such as, Covillea, Flourensia, Prosopis, and Acacia. Wooten & Standley (1912), in a discussion of grasses of New Mexico, show the San Augustin area as part of what they call a "Blue Grama Society" covering about three-fourths of the state. Cockerill, Hunter, & Pingrey (1939) include the grasslands of this area as part of the short grass plains dominated by blue, black, hairy and side-oats gramas with a yearlong grazing capacity from 10-30 animal units per section. In a map prepared from those of the Soil Conservation Service and the Forest Service, Dortignac (1956) refers to the grassland area of this region of New Mexico as "Grass and half shrubs (semi-desert)," although such shrubs as creosote bush (Larrea), saltbush and greasewood, sand sagebrush, and sagebrush are separately classified. Buffalograss

(Buchloe dactyloides) of the typical short grass plains to the east is not present.

To the writer's knowledge, the only study of the plains vegetation of the San Augustin basin is an unpublished density-yield study of reseeded and native vegetation by Springfield (1951). This study was conducted near the northeast end of the plains and just below the pinyon-juniper zone, 0.5 mi. west of the Monica Ranger Station. Plots were completely protected from both rabbits and cattle in contrast to the heavily grazed surrounding area. Blue grama in 1947 represented 83% of the herbage cover and 83% of the air-dry herbage yield. The 2-yr drought of 1949-51, a typical feature of the plains area, had a marked effect on the vegetation. The air-dry herbage yield in lbs/A for native grasses was reduced from 250 lbs in 1949 to 21 lbs in 1951. During the same period, the yield of introduced crested wheatgrass dropped from 426 lbs to less than 10 lbs. Although the yearly precipitation for 1951 was 11.8 in., most of it occurred after July, which was too late for the cool-season wheatgrass and was not greatly reflected in yield of native grasses because of their weakened condition and decreased density. The above example illustrates the importance of distribution of rainfall in this area of critical moisture. Great changes in density and herbage production do provide favorable grounds for the invasion of annual weeds with the resumption of normal moisture, a succession repeatedly observed in this and other areas.

In the lower areas the soils are alluvial and of intermediate to coarse texture, having originated as outwash from the surrounding hills. Intermixed with sands and fine gravels are commonly found many fragments of weathered volcanic rock. Here the alkalinity is low and drainage is good. The waters from the ephemeral streams of the surrounding embayments are lost by infiltration into these soils so that the basin itself is not traversed by stream beds. Water which reaches the lower playas does so by widespread surface flow, or by infiltration and seepage to the lower levels. The most prominent factor affecting growth vigor is this overflow water common to the mouth of canyons. Blue grama grass responds by producing fruiting stalks up to 3 ft in height. It must be these areas to which Cleaveland (1941) refers when she mentions cutting hay from the abundant native grama grass in the early days of settlement. Haying occurred in exceptional years, perhaps once in seven when she describes a whole canyon floor as "a mauve-and-purple carpet with a nap a yard deep." Today, the local residents tell of cutting hay in broad canyon floors as late as 25 yrs ago in areas which are now dominated by a dense cover of rabbitbrush *(Chrysothamnus* spp.).

There is a contrast in the zonation at the northeast and southwest ends of the plains. At the former end, pinyon-juniper woodland extends down the slopes of the surrounding hills and out into the adjacent basin. The lower elevation of the woodland is especially apparent in the Sand Hills area northeast of Augustine, but is generally true throughout the entire north end. In contrast, is the zonation of the south side of the southwestern end, in particular. Here, the slopes are more abrupt and very rough, with soils composed of coarse particles of weathered volcanic rock. One possible explanation of this difference lies in the sandier soils at the northern end which would have a more favorable soil moisture relationship. A second cause may be that suggested by a comparison of the climatological data for a 17-yr period at Augustine near the north end and for an 11-yr period at the Birmingham ranch near the south end. The average annual rainfall is 1.8 in. greater at Augustine.

This type is dominated by grasses of mixed form and height, with occasional areas where shrubs have invaded, or are distinctive of particular sites. Rabbitbrush is a common invader, particularly on overgrazed lower slopes and along stream terraces. Apache plume *(Fallugia paradoxa)* is common on coarse, gravelly, volcanic soils and is a distinctive plant of the beach ridges around the old lake bed. This plant may be found again at higher altitidues of greater precipitation and lower temperatures, but localized on exposed, rocky slopes. Watson (1912) also observed this distribution in the Sandia Mountains to the north. The species is the typical invading shrub of relatively recent lava flows, as at Sunset Crater, Arizona. Cacti are uncommon and are limited to a few scattered plants of the low growing types typical of mixed grasslands.

The lower slopes are relatively uniform in composition with some variations in the concentration of forbs apparently due to differences in rates of grazing in the past. Blue grama grass reaches its maximum dominance on lower slopes where in several stands it had frequencies of 100% in 100 quadrats. As in the saltbush-grama type, the stands on dune sand soils produced the greatest number of species, with as many as 7 species of forbs which were distinctive to these sites.

Total number of species was also high on stands located on the grass-covered volcanic hills near the south end of the basin. Here is a variety of slopes, exposures, and coarse soils with outeroppings of volcanic rock. One finds grass species here which are not common below, such as, black grama *(Bouteloua eriopoda)*, silver beardgrass *(Andropogon saccharoides)*, little bluestem *(Andropogon scoparius)*, and side-oats grama *(Bouteloua curtipendula)*. Several shrubby species are also found among the volcanic rocks, including skunk-bush *(Rhus trilobata)*, hoptree *(Ptelea angustifolia)*, and yerba-de-pasmo *(Baccharis pteronioides)*.

The mean herbage cover of this type is the highest of any of the associations, averaging 23% (Table 4), with a minimum of bare areas. The results from all stands in the type show blue grama to be the definite, dominant, producing about half of the total herbage cover. In some areas blue grama tufts measure up to 2 feet in diameter but show the effect of recent years of drought in addition to the natural death in the center of the tufts. Russian thistle and

false buffalograss *(Munroa squarrosa)* are subdominants. The increase of both is apparently related to the intensity of grazing, as are several species of forbs which are high on the listing by relative herbage cover. Sand dropseed is, of course, related to the extent of sandy soils within the type.

TABLE 4. Ground cover of herbs and shrubs in the Grama grassland zone based on 1000 1-sq. ft. quadrats.

Species	Cover		Frequency		Constance
	mean herb cover when present (0-5)	rel. herb cover %	freq. index %	rel. freq. %	%
Bouteloua gracilis	3.6	43.1	66	27.7	100
Salsola kali	2.3	20.0	51	21.4	70
Munroa squarrosa	1.7	10.6	34	14.3	90
Sporobolus cryptandrus	2.3	4.7	13	5.5	60
Amaranthus sp.	1.3	3.9	11	4.7	60
Aster arenosus	1.4	2.9	15	6.4	60
Aristida adscensionis	1.4	2.4	8	3.4	60
Sphaeralcea spp.	1.4	2.3	8	3.5	60
Zinnia grandiflora	1.7	1.4	4	1.8	50
Aristida divaricata	1.6	1.0	4	1.7	90
Psilostrophe sp.	3.2	1.0	2	.8	10

Summary of 10 sites (1000 quadrats)	Max.	Min.	Aver.	Total
Foliage cover (%)	31	12	23	....
Frequency of vegetated quadrats (%)	100	96	99	....
Total species per site	19	7	13	38+

Species with less than 1% relative herbage cover: *Descurainia obtusa, Dithyrea wislizeni, Bouteloua curtipendula, B. simplex, B. eriopoda, Chrysothamnus* sp., *Lycurus phleoides, Sporobolus contractus, Aristida longiseta, Abronia fragrans, Salvia subincisa, Androsace septentrionalis, Euphorbia* sp., *Gilia longiflora, Muhlenbergia torreyi, Acantkochiton wrightii, Andropogon scoparius, Chenopodium album, Eriogonum* spp., *Fallugia paradoxa, Haplopappus* sp., *Ambrosia artemisiifolia, Artemisia carruthii, Commelina dianthifolia, Monarda pectinata, Opuntia* sp., Misc. spp. unidentified.

The grazing value of lands in the area is in large part related to the vigor and composition of this type. The lower areas on the flats of heavy soils are occupied almost exclusively by alkali sacaton which has proven to be highly resistant to heavy utilization after the growing season. This grass species, locally called "Saltgrass," is undoubtedly the most valuable plant for winter and early spring range. The success of over-wintering cattle and the percentage of spring calf crop is to a large extent dependent on the availability of this grass for ranches having land within the old lake bed. Patches of Aparejo grass, saltgrass, and Juncus appear to be less valuable for grazing. Because of the distinctive character of the alkali sacaton on the silty clay flats, the extensive areas of sacaton are shown on the vegetative map as a subtype of the grassland. It covers a vast area of the low part of the basin.

Grazing recommendations for ranches of the area average about 10-12 head of cattle per section on a yearlong basis. However, several successful ranchers in the area, on good-condition grasslands, are stocking at a rate of 8 head per section. Proper distribution of livestock back into the hills, water development, and maintenance of some reserve areas for drought years are major problems in the area.

PINYON-JUNIPER ASSOCIATION

Although there are no studies of pinyon-juniper from western New Mexico, there are several studies of the type from other areas in the general region. This zone was included in a study of north-central New Mexico by Watson (1912) in which he separated a distinct pinyon formation from that of a lower woodland dominated by *Juniperus monosperma.* The zone is also included in a survey of farming and ranching areas of New Mexico by Cockerill, Hunter & Pingrey (1939). In studying the tension zone between grassland and woodland in northeastern New Mexico, Emerson (1932) considered climatic contrasts, edaphic differences, root distribution, ground cover, seed dispersal and reproduction.

The most extensive survey of the type was that of Woodin (1953) and that of Woodin & Lindsey (1954) in an analysis of stands by the line-strip method from Texas to central Colorado. Analysis of a "typical" station in eastern New Mexico showed that *Juniperus monosperma* composed 62% of the coverage and 63% of the abundance, while about one-third of the cover and abundance was of *Pinus edulis.* On this basis they suggest the use of "Juniper-pinyon," which had also been suggested by Daubenmire (1943) in referring to zones in the Rocky Mountains. The balance of the tree stratum was made up of species of *Quercus.* The foliage coverage of trees amounted to 12.9% of the ground area, while the average ground cover was 18.8%, about half of which was of grasses.

One of the most interesting features of Woodin & Lindsey's (1954) analysis is a discussion of the altitudinal trends of the principal species corrected to their "equivalent altitude" if all were located at the latitude of Albuquerque. Of the junipers, *Juniperus monosperma* is the principal dominant at lower altitudes, *J. scopulorum* reaches its maximum importance in a narrow zone between 6500 and 7000 ft elevation, *J. pachyphloea* increases in importance above this level and extends into the ponderosa pine type at about 7500 ft. Only at 7200 ft and above (about 20% of the zone) does *Pinus edulis* equal and surpass the *Juniperus* spp. in importance.

The dominance of juniper is also recognized by Woodbury (1947) in Utah as a juniper-pinyon type which meets ponderosa pine at 5000-7500 feet elevation.

The complex relationships between density, basal area, and cubic volume for this type, which includes trees of various forms, is given by Howell (1941) based on a study in northern New Mexico and northeastern Arizona. Volumes of one-seeded junipers having similar height, crown and trunk diameters varied as much as 7.5% volume of each other. While wood volume is not correlated to pollen production, which is a concern of this study, it does suggest the extreme difficulty of correlating any of the standard phytosociological attributes for species of such variable form. Howell (1941) established three types: (1) juniper, (2) pinyon, and (3) mixed, based on the

dominant having 60% or more of the basal area, or lack of either species to attain this percentage.

Many of the ecological requirements of pinyon have been discussed by Phillips (1909) in which article he points out its greater susceptibility to drought and frost in comparison with junipers. Inhibitive to its reproduction are the intervals between mast years and the high degree of infertility of its seeds.

A detailed phytosociological study of a pinyon-juniper community at Grand Canyon has been reported by Merkle (1952). At this latitude, pinyon is the most abundant tree above 6800 ft. A total of 18 species of understory plants was sampled.

In the San Augustin Plains, the pinyon-juniper zone occurs on a variety of sites, exposures, and soils. Some lower areas are on sandy, weathered soils washed down from surrounding slopes. Upper areas are often on coarse, rocky soils with large boulders and rocky, volcanic outcroppings. The percent of slope was measured with an Abney level at 100-ft intervals along each elb. The maximum elb average was 54%, the minimum 3%, and the average slope for all elbs was 22%. Strict zonation according to elevation did not apply in much of the area due to the greater influence of slope exposure, the desiccation of southwestern winds and the lack of snow accumulation and retention. Pinyon and juniper often topped the ridges and extended a short distance down the opposite slope.

Evidence of a series of drought years is present in all stands, but greater damage is generally evident in rocky exposures than on finer soils of lower areas. Pinyon shows greater drought injury than the accompanying junipers. A large percent of the Gray oak *(Quercus grisea)* patches also show severe drought damage.

Mature tree stratum.—The phytosociological analysis of the tree stratum, based on the line-strip, method, is summarized in Table 5. All plants of 4 in. or more diameter are included. It was felt that relative foliage cover was the most important attribute in this study, and the species are arranged in order of decreasing value on this basis. Most striking is the dominance of pinyon *(P. edulis)* which makes up 60% of the foliage cover and twice as much as the codominant—alligater juniper *(Juniperus deppeana)*. A general view of this type is shown in Fig. 9. Gray oak might be considered a subdominant, occupying a position as a tall shrub and occurring in many-stemmed thickets. One-seeded juniper occupies a minor position. The general lack of importance of one-seeded juniper is in great contrast to results of a study of Woodin & Lindsey (1954) from eastern New Mexico where the ratio of foliage cover of one-seeded juniper to pinyon was about 1:0.5, while here it is about 1:37. One-seeded juniper occurs only along the very lower edges of the zone, or is often completely absent. It is more common near the northeast end of the plains where an open woodland extends out into the plains on gentle sandy slopes. The foliage cover of all trees expressed as ground cover was nearly identical to the above study, being 12% for the San Augustin Plains area. The importance of alligator juniper, recognized as replacing other junipers at increasing altitudes and into ponderosa pine zone, is evidenced here where the pinyon-juniper zone ranges from about 7000 to 9000 ft in elevation. At the latter elevations the type is found on south and western exposures and on exposed ridges.

The relationship of density for the two dominants is nearly the same as that of foliage cover, with 57% of the trees represented by pinyon and 27% by alligator juniper. However, the ratios for foliage cover and density are nearly reversed when relative basal area is considered. Here alligator juniper exceeds with 54% compared to 35% for pinyon. Very old and large alligator junipers are common. One tree in the sampled area measured 41 in. in diameter at the 1-ft height. The average trunk diamenter for trees of 4 in. or greater diameter was

TABLE 5. Mature tree stratum of pinyon-juniper zone. All values are based on plants of 4 in. or greater diameter at the 1-ft height. Cover is based on line intereception, density and basal area on a 20-ft strip, and frequency on 480 20×50 ft quadrats of 30 elbs, each 800 ft long.

Species	Cover				Density		Basal Area		Frequency	
	rel. fol. cover %	ground cover %	foliage per acre sq. ft.	mean crown diam. ft.	rel. dens. %	dens. per acre	rel. basal area %	sq. ft. per acre	freq. index %	rel. freq. %
Pinus edulis	59.7	7.1	3105.8	10.8	57.0	33.9	34.7	8.7	39.6	49.1
Juniperus deppeana	29.8	3.6	1546.4	11.0	27.3	16.2	54.2	13.6	24.4	30.3
Quercus grisea	6.0	.7	313.6	7.7	11.9	7.1	8.5	2.1	10.6	13.1
Pinus ponderosa	1.9	.2	100.2	17.9	.8	.4	.9	.2	1.0	1.2
Juniperus monosperma	1.6	.2	87.1	8.9	2.3	1.4	.?	.?	1.9	2.4
Quercus undulata	.3	< .1	17.4	13.6	1.1	1.2	.6	.2	1.5	1.9
Quercus gambelii	.3	< .1	13.1	12.9	.2	.1	.4	.1	.2	.2
Cercocarpus breviflorus	.2	< .1	13.1	6.4	.8	.4	.3	.1	1.0	1.2
Juniperus osteosperma	.2	< .1	13.1	9.1	.3	.2	.3	.1	.4	.5
Total		11.96	5209.8			60.9		25.0		

FIG. 9. General view of pinyon-juniper vegetation on a typical slope of thin soils and dominant blue grama cover.

12.4 in. for alligator juniper in contrast to 6.9 in. for pinyon. Because of the habit of multiple branching from and below the ground level, which is a characteristic of one-seeded juniper, no estimates of stem diameter were included for this species. The number of trees involved was low, and their omission affects but slightly the total or relative basal area figures.

Of specific interest was the distribution of Rocky Mountain juniper *(J. scopulorum)*. This species is very common in the Datil Mountains at the north end of the Plains. It appears to be the principal transition tree between the pinyon-juniper and the ponderosa pine zones. The species did not occur in any of the sample areas at the southwest end of the plains, nor does the writer recall seeing it in that area. It is difficult to postulate a reason for the southward limit of distribution, as there are comparable elevations, climatic conditions, and soil types in both areas.

Table 5 shows that an average acre of ground of this type supports about 61 trees with a total foliage cover of 12% or 5210 sq. ft and basal area of 25 sq. ft. Of these attributes, the two dominants (pinyon and alligator juniper) comprise about 84% of the density, 90% of the foliage cover, and 89% of the basal area.

SAPLING AND BRUSH STRATUM

The results of the analysis of the reproductive strata of trees and shrubs over 3 ft in height but less than 4 in. in stem diameter are given in Table 6. The species are arranged in order of decreasing relative foliage cover. Except for a reversal of ponderosa pine and one-seeded juniper, with only slight differences, the order of species is the same as in the tree stratum. The total ground cover of all species is about 3% in contrast to the 12% of the overstory. The importance of pinyon in the reproductive strata is especially pronounced, being 10 times that of alligator juniper. This great importance is in contrast to the mature stratum where pinyon is only twice as important. This ratio is decreased for relative density of trees wherein pinyon exceeds alligator juniper by a ratio of 7:1. Gray oak is of increasing importance in this stratum because of its shrubby growth form. All other species are of minor importance, but include shrubs, such as *Ribes* spp., *Fallugia paradoxa*, *Philadelphus microphyllus*, and *Rhus trilobata* not present in the overstory.

HERB AND SEEDLING STRATUM

All of the pinyon-juniper stands in the San Augustin Plains are above 6800 ft and, as has been pointed out, the importance of pinyon reflects the effects of this elevation. The understory vegetation of this woodland type for this area is relatively low in herbage cover, 15%, but it is high in number of species 58+, as is shown in Table 7. The sparse vegetative cover in the open spaces of the woodland is composed of scattered, small tufts of grasses which develop on the thin often rocky soils. That the cover is an extension of the mixed grassland below is evidenced by a comparison of the species lists of Tables 4 and 7, which shows that all except 7 out of 38 species from

TABLE 6. Sapling and brush stratum in the pinyon-juniper zone over 3 ft in height but less than 4 in. stem diameter at the 1-ft height. Cover is based on line interception, density on a 20-ft strip, and frequency on 480 20×50 ft quadrats of 30 elbs, each 800 ft long. Seedling frequency is based on 1000 1-ft quadrats.

Species	Cover			Density		Frequency		Seedling
	rel. fol. cover %	ground cover %	foliage per acre sq. ft.	rel. dens. %	dens. per acre	freq. index %	rel. freq. %	freq. index. %
Pinus edulis	82.1	2.3	988.8	74.2	78.8	78.2	56.0	.1
Juniperus deppeana	8.1	.2	100.2	10.5	11.2	26.3	18.8	.1
Quercus grisea	5.6	.2	65.3	9.3	9.9	16.7	11.9	.2
Juniperus monosperma	2.0	< .1	4.4	.7	.7	2.2	1.6	..
Pinus ponderosa	1.2	< .1	13.1	.8	.8	1.9	1.3	..
Quercus undulata	.5	< .1	4.4	.1	.1	.4	.3	..
Cercocarpus spp.	.3	< .1	4.4	2.8	3.0	8.9	6.4	..
Ribes spp.	.3	< .1	4.4	.7	.7	1.9	1.3	..
Fallugia paradoxa	..	....	...	.2	.2	.7	.5	..
Juniperus osteosperma	..	....	...	.3	.3	1.1	.8	.2
Philadelphus microphyllus	..	....	...	.5	.5	.7	.5	..
Rhus trilobata	..	....	...	.2	.2	.7	.5	..
Total		2.7	1184.9		106.2			

the grassland are represented in the pinyon-juniper association. These 7 species were of rare occurrence and of very minor importance in the grassland. They, of course, may also be present in the woodland in small amounts and were not included in the sampling.

TABLE 7. Ground cover of herbs and woody plants less than 3 ft in height in the pinyon-juniper zone based on 1000 1-sq. ft. quadrats.

Species	Cover		Frequency		Constance
	mean herb cover when present (0-5)	rel. herb cover %	freq. index %	rel. freq. %	%
Bouteloua gracilis	3.9	26.9	59	26.9	100
Chenopodium incisum	2.7	13.6	28	12.9	100
Salsola kali	2.8	13.2	27	12.3	70
Aster arenosus	1.4	8.2	30	7.3	100
Munroa squarrosa	2.1	6.1	16	3.7	70
Aristida adscensionis	1.8	3.7	8	2.5	80
Sporobolus cryptandrus	1.8	2.0	6	1.1	50
Mirabilis multiflora	2.8	1.2	3	1.1	50
Bouteloua hirsuta	3.5	1.1	2	2.9	50
Salvia subincisa	1.0	1.1	6	1.4	40
Chenopodium album	1.7	1.0	3	1.0	50
Descurainia obtusa	2.0	1.0	2	...	30

Summary of 10 sites (1000 quadrats)	Max.	Min.	Aver.	Total
Foliage cover (%)	23	10	15	....
Frequency of vegetated quadrats (%)	99	89	96	....
Total species per site	27	12	19	58+

Species with less than 1% relative herbage cover: *Lycurus phleoides, Aristida divaricata, A. longiseta, Amaranthus* sp., *Sphaeralcea* spp., *Juncus* sp., *Bouteloua curtipendula, B. eriopoda, B. simplex, Allium* sp., *Bahia dissecta, Festuca arizonica, Sporobolus contractus, S. microsperma, Carex* sp., *Dithyrea wislizeni, Eriogonum* sp., *Gilia longifolia, Mimosa* sp., *Monarda pectinata, Muhlenbergia torreyi, M. montana, Cerastium* sp., *Chrysothamnus* spp., *Euphorbia* sp., *Gutierrezia lucida, Androsace septentrionalis, Zinnia grandiflora, Viguiera multiflora, Artemisia caruthii, A. frigida, Aster hirtifolius, A. commutatus, Atriplex canescens, Bouteloua barbata, Opuntia* sp., *Oryzopsis micrantha, Physalis pubescens, Sitanion hystrix, Yucca* sp., Misc. spp. unidentified.

Of the 7 most important species in each type, 6 are common to both types. The large species list, greater than that of any of the lower elevation types, is the result of the variety of sites resulting from slope exposures, shade, drainage and a mixture of soil textures. There are, for example, 6 more species of grasses than in the grassland below. Of the 19 species of grasses only blue grama is of major importance, however. It alone makes up nearly half of the understory herbage cover. Secondary to it are *Chenopodium incisum* and Russian thistle. *Chenopodium incisum* is the most abundant plant under the shade of the pinyon and junipers. The four-o'clock *(Mirabilis multiflora)* occupies a similar habitat but of less importance. Russian thistle has invaded the open, grassy slopes not unlike those of grassland below.

PONDEROSA PINE ASSOCIATION

The ponderosa pine forest of the San Augustin Plains drainage is generally an open type of stand with a limited amount of underbrush. The type occurs at its lowest elevation near the northeast end of the plains where it follows an area of sandy soil down to the upper edge of the grassland. Here on gentle slopes about 6 ft of sand overlies a clay subsoil resulting in favorable moisture conditions which allow growth at lower elevations than in surrounding areas of rocky soils. Upper areas of the zone are usually on rocky soils of steeper slope. The average percent of slope for each elb varied from 5% to 56% with an average for all elbs of 27%. This average slope is only several degrees higher than that of the pinyon-juniper zone. Often the two types are represented on opposite sides of the same canyon with similar slope and soil but different exposures. The greatest portion of ponderosa pine forest in the drainage area is composed of those stands located up the major canyons and on broad northern and eastern slopes.

At the present time a major salvage cutting operation is in action in the area in the pine forest. Successive years of drought have weakened trees to such an extent that they are unable to withstand an infestation of bark beetles. In many areas, few healthy seed-producing trees are left. What will happen to the remaining generally healthier young stock, which will be exposed to an intensified attack with the removal of other trees, remains to be seen. The removal of much of the overstory will also favor the development of the understory plants such as pinyon pine, Gambel oak *(Quercus gambelii)*, gray oak, and alligator juniper in addition to a variety of shrubs.

The best ecological discussion of the ponderosa pine forest for western New Mexico including climate, soils, and vegetation is that of Pearson (1931).

MATURE TREE STRATUM

The phytosociological analysis of the mature tree stratum, based on the line-strip method, is summarized in Table 8. The importance of ponderosa pine is illustrated by the percent of vegetational cover which is 74%, almost 8 times that of pinyon, the nearest cover competitor. Because the purpose of this study was to depict the present vegetation in relation to its present pollen production and its dispersal into various areas of the drainage basin, no selection of sites was made in regard to presence, absence, or recency of lumbering. The sites for sampling were randomly selected. Two sites had recently been selectively lumbered. In one elb there was nearly complete death of mature ponderosa pine due to drought damage resulting in a lower cover of this species than in any other area. In this site, pinyon was the definite dominant. An area of the type showing only moderate drought and beetle damage is illustrated in Fig. 10. Pinyon and alligator juniper, co-dominants of the zone below, occupy positions of secondary importance in respect to foliage cover. Gambel oak, Douglas fir *(Pseudotsuga taxifolia)*, and gray oak were nearly equal in foliage cover. Gray oak occupies a position on ridges and on dry exposures. Gambel oak, considered typical understory in ponderosa pine, is generally found on canyon slopes in conditions of intermediate moisture in the

TABLE 8. Mature tree stratum of ponderosa pine zone. All values are based on plants of 4 in. or greater diameter at the 1-ft height. Cover is based on line interception, density and basal area on a 20-ft strip, and frequency on 480 20×50 ft quadrats of 30 elbs, each 800 ft long.

Species	Cover				Density		Basal Area		Frequency	
	rel. fol. cover %	ground cover %	foliage per acre sq. ft.	mean crown diam. ft.	rel. dens. %	dens. per acre	rel. basal area %	sq. ft. per acre	freq. index %	rel. freq. %
Pinus ponderosa	73.9	13.3	5810.9	13.7	58.7	39.6	71.2	28.8	45.0	56.1
Pinus edulis	9.5	1.7	749.2	9.9	14.4	9.7	6.3	2.6	10.2	12.7
Juniperus deppeana	5.3	1.0	413.8	15.0	3.5	2.4	11.6	4.7	4.6	5.7
Quercus gambelii	3.4	.6	270.1	6.1	13.7	9.2	5.7	2.3	11.7	14.6
Pseudotsuga taxifolia	3.3	.6	261.4	9.7	2.7	3.6	1.9	.8	1.9	2.3
Quercus grisea	3.1	.6	248.3	9.3	5.4	3.6	2.5	1.0	4.6	5.7
Pinus flexilis	1.2	.2	91.5	15.8	.8	.5	1.7	.7	1.3	1.6
Cercocarpus breviflorus	.2	< .1	17.4	6.5	.8	.5	.2	.1	1.0	1.3
Total		18.1	7862.6			69.0		41.0		

type. Douglas fir is limited to small stands on steep, northfacing slopes and near the heads of canyons, in habitats providing wind protection, higher precipitation, or seepage water. Limber pine *(Pinus flexilis)* is often found with Douglas fir or occasionally isolated trees with ponderosa pine along canyon stream bottoms. Trees in such sites have low frequency and density with relatively high basal area and coverage values. The total ground cover of all mature tree species was 18%, of which 13% was that of ponderosa pine.

FIG. 10. Ponderosa pine type on gently sloping, sandy soils showing sparsity of understory vegetation but with small patches of pine reproduction.

The importance of ponderosa pine in density is somewhat less than for coverage. The species makes up about 59% of the mature trees. The more slender form of pinyon is evidenced by narrow crown diameter, high density, low basal area, and high frequency. In contrast, the figures for alligator juniper indicate its broad, rounded foliage form and predominance of large trunks of mature plants. Its ratios to ponderosa pine for foliage cover are 1:14, for mean crown diameter 1:0.9, for density 1:17, and for basal area 1:6. One tree of alligator juniper measured 43 in. in diameter. The average trunk diameters for the principal species of mature trees were: ponderosa pine—11.6 in., pinyon—7.0 in., alligator juniper—19.1 in., and Gambel oak—6.8 in.

The analyses show an average acre of this type to be dominated in all attributes by ponderosa pine with secondary trees of pinyon, alligator bark, and Gambel oak. The acre would support 69 mature trees of all species with a total foliage cover of 18% or 7863 sq. ft and a basal area of 41 sq. ft. Of these attributes, ponderosa pine comprises 59% of the density, 74% of the foliage cover, and 71% of the basal area.

SAPLING AND BRUSH STRATUM

Data for the sapling and brush stratum are given in Table 9. The dominance of ponderosa pine is less evident in this stratum with a relative foliage cover of 31% than in the overstory where relative foliage cover is 74%. This reduction is due principally to the increase in importance of Gambel oak, as well as pinyon and Douglas fir. The reduction in importance of ponderosa pine reproduction is in sharp contrast to the increased importance of pinyon reproduction in the piyon-juniper zone. Ponderosa pine has a relatively high frequency in the sapling stratum which indicates good distribution and that reproduction is of greater importance than is often attributed to it. Large patches of reproduction commonly occur with the advantage of decreased slope, increased moisture and sandier soils found at the base of canyon slopes. The total understory ground cover of 4% is similar to that of the pinyon-juniper zone. The ratio of number of reproductive trees and shrubs to mature plants is about 3:1 in the ponderosa pine type in contrast to 4:1 in the pinyon- juniper zone. As would be expected, there is a greater conformity between the values for foliage cover and density in the sapling and brush stratum than in the mature stratum.

TABLE 9. Sapling and brush stratum in the ponder osa pine zone over 3 ft in height but less than 4 in. stem diameter at the 1-ft height. Cover is based on line interception, density on a 20-ft strip, and frequency on 480 20×50 ft quadrats of 30 elbs, each 800 ft long. Seedling frequency is based on 1000 1-ft quadrats.

Species	Cover			Density		Frequency		Seedling
	rel. fol. cover %	ground cover %	foliage per acre sq. ft.	rel. dens. %	dens. per acre	freq. index %	rel. freq. %	freq. index. %
Pinus ponderosa	30.9	1.1	479.2	31.8	61.4	49.0	29.0	.5
Quercus gambelii	21.7	.8	339.8	31.1	60.1	35.8	21.2	1.2
Pinus edulis	17.5	.6	274.4	13.3	25.6	38.9	23.0	.6
Pseudotsuga taxifolia	13.0	.5	204.7	12.1	23.4	4.9	2.9	...
Juniperus deppeana	5.6	.2	87.1	4.1	8.0	14.2	8.4	...
Quercus grisea	4.8	.2	74.1	2.4	4.7	8.0	4.7	.3
Pinus flexilis	3.2	.1	52.3	1.0	2.0	3.8	2.3	...
Holodiscus dumosus	1.3	.1	21.8	.9	1.8	1.7	1.0	...
Philadelphus microphyllus	.7	< .1	13.1	.9	1.6	2.1	1.2	.1
Cercocarpus spp.	.6	< .1	8.7	.7	1.3	4.5	2.7	...
Ribes spp.	.3	< .1	4.4	.5	.9	3.5	2.1	...
Abies concolor	.1	< .1	1.7	.1	.1	.4	.2	...
Quercus undulata	.1	< .1	1.7	.3	.6	.7	.4	...
Fallugia paradoxa	..	....	...	.7	1.3	1.0	.6	.2
Jamesia americana	..	....	...	.1	.1	.4	.2	..
Juniperus osteosperma	..	....	...	.1	.1	.4	.2	..
Total		3.6	1562.9		192.8			

The increased number of species in the understory (16 in contrast to 8 in pinyon-juniper) is noteworthy. *Pinus flexilis, Abies concolor, Holodiscus dumosus, Jamesia americana,* and *Ribes* spp. are common to the ponderosa pine type, apparently favored by conditions of increased moisture. Seedlings of Gambel oak are about twice as frequent as ponderosa pine or pinyon.

HEBB AND SEEDLING STRATUM

The analysis of the herbaceous and seedling stratum is given in Table 10. The herbage cover of 12% is lower than for the pinyon-juniper zone and there is a variation between stands from 7% to 24%. The frequency of vegetated quadrats per stand was also lower, averaging 83%. However, under the more favorable moisture conditions and cooler temperatures, the number of species in this zone was greater than in the woodland, averaging 22 per stand and a total list of about 80 species. This list would have been even greater had it been possible to sample the herbaceous cover following the midsummer rains rather than at their beginning. The pinyon-juniper zone had been sampled at the end of the previous growing season.

On the basis of relative cover, the two grasses, mountain muhly *(Muhlenbergia montana)* and blue grama grass compose nearly two-thirds of the cover. Mountain muhly here replaces blue grama as the dominant, exceeding the latter by twice the coverage. The five most important species are all grasses, including the above plus Arizona fescue *(Festuca arizonica)*, prairie junegrass *(Koeleria cristata)*, and pine dropseed *(Blepharoneuron tricholepis)*. These five amount to 80% of the herbaceous cover and provide the principal forage which makes the pine forest a valuable summer grazing range. The total list of species includes at least 18 of grasses, 12 of composites, and 8 of legumes.

TABLE 10. Ground cover of herbs and woody plants less than 3 ft in height in the Ponderosa pine zone based on 1000 1-ft quadrats.

Species	Cover		Frequency		Constance
	mean herb cover when present (0-5)	rel. herb cover %	freq. index %	rel. freq. %	%
Muhlenbergia montana	4.1	41.9	48	33.6	100
Bouteloua gracilis	3.8	21.4	26	18.2	90
Festuca arizonica	3.1	11.1	17	11.5	100
Koeleria cristata	2.8	3.9	6	4.5	80
Blepharoneuron tricholepis	2.3	2.0	4	2.9	70
Andropogon sp.	3.3	1.5	2	1.5	60
Artemisia sp.	1.8	1.5	4	2.7	80
Sitanion hystrix	2.8	1.5	3	1.7	70
Muhlenbergia dubia	4.5	1.3	1	1.0	40
Carex sp.	3.3	1.2	2	1.2	50

Summary of 10 sites (1000 quadrats)	Max.	Min.	Aver.	Total
Foliage cover (%)	24	7	12	....
Frequency of vegetated quadrats (%)	95	61	83	....
Total species per site	37	11	22	80+

Species with less than 1% relative herbage cover: *Quercus gambelii, Q. grisea, Andropogon scoparius, Aristida arizonica, A. divaricata, A. ternipes, Chenopodium incisum, Astragalus* sp., *Berberis repens, Aster arenosus, Chenopodium album, Erigeron* sp., *Solidago* sp., *Sphaeralcea* spp., *Viguiera* spp., *Agropyron* sp., *Arabis* sp., *Chrysothamnus* sp., *Cirsium* sp., *Achillea lanulosa, Allium* sp., *Aplopappus* sp., *Ceanothus fendleri, Cercocarpus* spp., *Geranium* sp., *Heuchera* sp., *Lappula* sp., *Lathyrus* sp., *Linum neomexicanum, Hymenoxys richardsonii, Lotus* spp., *Muhlenbergia wrightii, Oxytropis lambertii, Pinus ponderosa, P. edulis, Senecio* spp., *Vicia* sp., *Antennaria* sp., *Bromus* sp., *Lupinus* sp., *Pseudocymopterus montanus, Draba* sp., *Eriogonum* sp., *Fallugia paradoxa, Galium* sp., *Lesquerella* sp., *Lithospermum* sp., *Lycurus phleoides, Philadelphus microphyllus, Poa* sp., *Thalictrum* sp., *Tragia* sp., *Mimosa* sp., *Muhlenbergia neomexicana, Penstemon* sp., *Plantago purshii, Potentilla* sp., *Thermopsis pinetorum, Thlaspi fendleri, Verbena* sp., Misc. spp. unidentified.

ANALYSIS OF SAMPLING OF WOODLAND AND FOREST TYPES

The writer deems it essential to add a short explanation of the relation between the sampling technique used in the woodland and forest types and the usual statistical analysis employed as a test of adequacy of sampling. The principal problem appeared to be one of obtaining as adequate a picture as possible of the forest types in a 180° arc around the southwest end of the Plains. Observation of the inherent variations and experience in actual field sampling indicated conclusively to the writer and to an experienced assistant that a large number of samples should be used and that they should be well distributed across the area. Time and money limited the number of samples which could be obtained. These factors allowed for 30 elbs each 800 feet long for each vegetative type. Surely a better indication of the entire area was obtained by the use of 3 elbs at each of 10 sites than, for instance, the use of 10 elbs at 3 sites. However, if one desired to show satistically a high degree of sampling adequacy, he could best do so by the latter arrangement. Actually, the statistical analysis would show the most adequate sampling if all 30 elbs had been located at one site.

To give some idea of the statistical results for adequacy of sampling, all of the 30 elbs of the 10 sites were considered as one group. The mean for any particular factor being considered was obtained as an average for all trees of that species in the entire sampled area. The standard error is expressed as a plus or minus figure indicating the range within which there is a 67% probability that the true value for the mean will occur. In general usage, if the standard error does not exceed 20% of the mean, the sampling has been adequate for that species. This relationship is indicated by the percent of error.

A comparison of the statistical analyses of several phytosociological attributes for the dominant tree species in the pinyon-juniper woodland and ponderosa pine forest, is summarized in Table 11. Here is given an analysis of the mean line-cover per elb (representing the interceptions for a given species for one elb line), of the mean density per elb (representing the number of trees for a species per strip 20 x 800 ft), and of the mean basal area for mature trees per elb (representing trunk area for a species within a strip 20 x 800 ft). The data are presented separately for reproductive trees over 3 ft in height but less than 4 in. in diameter. The statistical analyses indicate that in the mature trees of the pinyon-juniper zone only *Pinus edulis* was adequately sampled for line-cover, density, and basal area. In the sapling and brush stratum the only adequate sampling was for the density of *Quercus grisea*. This species is widely dispersed as an understory plant.

In the ponderosa pine zone, the statistical analyses indicate that the only adequate sampling was for density and basal area of *Pinus ponderosa*. In the sapling and brush stratum, only the sampling for *Pinus edulis* line-cover was adequate.

DOUGLAS FIR STANDS

Some of the isolated larger stands of this type are shown on the vegetation map, (Fig. 1). Within the drainage of the San Augustin Plains, however, this type is of very minor importance and no detailed studies were made of its composition. There are no extensive slopes of this type, but rather it is localized to the high altitude and deep canyons. Such a local stand is shown in Fig. 11 on a steep, rocky, north-facing canyon wall. Such areas may well be considered as faciations of the ponderosa association. The dominant here is Douglas fir, as it is in all such stands in the Plains drainage. The U. S. Forest Service labels these areas as Mixed Conifer where any one species or combination of conifers other than ponderosa pine or pinyon and junipers produces more than 50% of the timber volume. These are areas of longer retention of snow in the spring, and the presence of aspen as in Fig. 11, is often correlated with seepage water.

Understory plants of these areas are not unlike those of the adjacent ponderosa pine forest. Local sites are more moist as is indicated by the presence of an increased amount of moss and the presence of ferns.

Occasionally limber pine occurs in sites of plenti-

TABLE 11. A statistical analysis of adequacy of sampling considering all 30 elbs at 10 stations as one group. The mature tree stratum and sapling and brush stratum are treated separately.

	MATURE TREES									REPRODUCTIVE (3′ HEIGHT TO 4″ D. B. H.)					
	mean line-cover (ft.)	stand. error	% error	mean density per elb	stand. error	% error	mean basal area (sq. ft.)	stand. error	% error	mean line-cover (ft.)	stand. error	% error	mean density per elb	stand. error	% error
PINYON-JUNIPER ZONE															
Pinus edulis	57.0	± 8.9	15.6	12.5	±2.0	16.3	3.2	± .5	17.1	18.1	±4.5	25.0	29.1	±7.4	25.6
Juniperus deppeana	28.5	± 7.1	24.7	6.0	±1.5	24.8	4.7	±1.3	28.2	1.8	± .7	37.3	4.1	±1.4	33.5
Quercus grisea	5.7	± 2.4	41.5	2.6	±1.0	39.0	.8	± .3	40.0	1.2	± .6	49.8	3.6	± .6	17.0
PONDEROSA PINE ZONE															
Pinus ponderosa	106.7	±32.3	30.2	14.5	±2.1	14.6	10.6	±1.2	11.2	8.9	±2.4	26.8	22.6	±5.9	26.3
Quercus gambelii	4.9	± 1.7	34.3	3.4	±1.1	31.9	.8	± .3	34.2	6.2	±2.5	40.8	22.1	±8.3	37.7
Pinus edulis	13.7	± 6.5	47.2	.9	± .5	50.8	5.0	±1.6	31.8	9.4	±1.1	11.3	.9	± .3	38.2
Juniperus deppeana	7.6	± 3.5	46.0	.9	± .3	38.2	1.7	±1.2	70.4	1.6	± .7	44.9	2.9	±1.3	44.3

FIG. 11. A Douglas fir stand with an admixture of trembling aspen on a typical steep, rocky, north-facing canyon wall surrounded by ponderosa pine.

ful soil moisture. Both mature plants and reproduction were included in the sampling of the ponderosa pine zone where the elbs crossed steep-walled, moist canyons. Also included in the sapling stratum was a second conifer associated with Douglas fir, namely, white fir *(Abies concolor)*. The number of mature trees of this species is very low, although occasional reproductive size plants may be found in sites of most favorable moisture. No trees of Engelmann spruce *(Picea engelmanni)* or blue spruce *(P. pungens)* were found in the drainage of the San Augustin Plains even with the assistance of foresters in the area. Oddly enough, there are stands of Englemann spruce close to the plains drainage to the east and south. In the upper part of Beartrap Canyon, a south-facing canyon, of the San Mateo Mountains, is a stand of several acres of Englemann spruce with an admixture of aspen. The site is favored by the presence of seepage water at the bottom of the canyon. A few miles farther east on the east and north-facing slopes of Baldy Peak of the Magdalena Mountains are several small stands of Englemann spruce with a larger area of Douglas fir and some white fir below. There is a stand of about 1000 A of spruce near Bearwallow Mtn. about 14 mi. southwest of the end of the plains drainage.

SURROUNDING FORESTS

In addition to the detailed studies which are presented here from the line-strip analysis of the forest areas within the drainage of the southwest end of the plains, the following information presents a broader picture of a larger area lying to the southwest. It is certainly not the intention even to suggest that the source of pollen carried into the basin is limited to the drainage or watershed of the San Augustin Plains. However, some limit to the area studied and mapped was essential; and it appeared that the Continental Divide of the west and south sides, which corresponded to the edge of the plains drainage, was a logical boundary. A general picture of the forested area to the southwest has been provided by the Timber Management Division of the U.S. Forest Service regional office in Albuquerque. The Elk Mountain working circle, which corresponds closely to the Elk Mountain Ranger District, extends southwestward from the drainage of the plains for a distance of about 28 mi. and includes 325,400 A on which the proportions of forest are as follows:

Sawtimber (56%)

49% Ponderosa pine

7% Mixed conifer, including mostly Douglas fir and limber pine mixed with ponderosa pine. It is estimated that there is only about 1000 A of spruce, and practically all of it is at the southern edge of the district near Bearwallow Mtn.

Non-sawtimber (44%)

0.1% Aspen

12% Pinyon-juniper woodland

32% Non-timbered, brush, grass, or having less than 10% conifer cover.

SUMMARY

The study is a part of a project on the history of the San Augustin Plains as determined from palynological evidence of a 645-ft drill core near the center of the basin. Reported here is the distribution and composition of the vegetational types within the drainage basin, and a discussion of pertinent climatic and edaphic factors. This paper will be followed by a later report on the correlation of the present-day pollen rain into the basin at a number of sites to determine the distances of transport of pollen; relative abundance of pollen in relation to forest composition, cover, and density; and relative preservation of pollen in various media of the basin.

The San Augustin Plains is a high-altitude, intermontane, Pleistocene lake bed in western New Mexico surrounded by volcanic mountains. The general climatic conditions are semi-arid and microthermal, with principal precipitation in July and August and prevailing southwestern winds. The soils vary from silty clay of pH 9+ in the flats of the basin to the coarse soils and rocky volcanic slopes of the surrounding mountains.

The herbaceous and seedling stratum of each vegetational type was sampled by 100 1-sq. ft quadrats at each of 10 sites. Record was made of the total foliage cover and relative foliage cover per species. In the timbered areas, the sapling and brush stratum and mature tree stratum were sampled by the line-strip method, which yields data for frequency, density,

foliage cover, and basal area. Each type was represented by 30 line-strip elbs, each 800 feet long.

The following list gives the vegetational types of the area and the percent of area occupied by each type: greasewood-seepweed (1.6%), saltbush-grama (9.3%), grama grassland (41.7%) including a subtype of alkali sacaton (3.9%), pinyon-juniper (31.5%), ponderosa pine (15.8%), and local stands of Douglas fir (0.9%). The distribution of these types is shown on a vegetational map.

The greasewood-seepweed association, dominated by *Sarcobatus vermiculatus* and *Suaeda suffrutescens*, is limited to alkaline, silty clay soils. Occasional patches of *Sporobolus airoides*, *Muhlenbergia utilis*, and *Distichlis stricta* provide a sparse understory forage. Large soil cracks are distinctive of the area.

Patches of the saltbush-grama association, dominated by *Atriplex canescens* and *Bouteloua gracilis*, are found on sandy soils. The average herbage cover was 18%. The mixture of grass and saltbush provides a valuable combination forage for cattle.

The largest association is that of grama grassland on well-drained soils surrounding the basin. The dominant, blue grama, comprises about half the total herbage cover of 24%. *Salsola kali* and *Munroa squarrosa* are subdominants. On low-lying flat areas of heavier soils, alkali sacaton becomes dominant.

The pinyon-juniper woodland association exhibits the characteristics of a high altitude woodland of 7000-9000 ft elevation. *Pinus edulis* is the dominant of the zone. Of the 12% total overstory cover, pinyon composes 60% and *Juniperus deppeana* about 30%. The ratios are about the same for density, but alligator juniper exceeds pinyon in basal area due to the many large and old trees. *Quercus grisea* is the principal understory plant. *J. monosperma* is of minor importance, being limited, when present, to the lowest edges of the zone.

The relative coverage and relative density of pinyon reproduction are even greater than in the overstory stratum. Alligator juniper and gray oak are of secondary importance in the understory cover. The total cover of this stratum equals 3%.

The herbaceous vegetation of the pinyon-juinper zone is comparable in species to the grassland below, with some additional species due to the variety of microhabitats. The total herbage cover was 15% with a total of more than 58 species represented. *Bouteloua gracilis* was dominant, followed by *Chenopodium incisum* and *Salsola kali*.

The ponderosa pine forest association is found principally on east and north-facing slopes, and extending downward along canyon bottoms and on areas of sandy soils with more favorable moisture relations. Successive years of drought and a bark beetle infestation have greatly reduced the stand of mature timber in many areas. Of the 18% of total overstory cover, *Pinus ponderosa* composed 74%, *Pinus edulis* 10% and *Juniperus deppeana* 5%. *Pinus ponderosa*, the dominant, comprises 59% of the density and 71% of the basal area.

Ponderosa pine is less important in the sapling and brush stratum due to an increase in importance of Gambel oak, pinyon, and Douglas fir. There is an increase in number of species in this stratum over that of the pinyon-juniper zone below.

The herbaceous cover of this zone is dominated by *Muhlenbergia montana* and *Bouteloua gracilis*, which together equal about two-thirds of the cover. The five most important species are grasses.

Douglas fir stands are localized on deep, high-altitude canyons and on steep, north-facing, rocky slopes of more mesic conditions than the surrounding area. Neither *Picea engelmanni* or *P. pungens* were found in the drainage of the San Augustin Plains, although there are several stands outside the drainage to the east and south.

LITERATURE CITED

Antevs, E., 1954. Climate of New Mexico during the last glacio-pluvial. Jour. Geol. **62:** 182-191.

Bryan, K. 1926. Ground water reconnaisance in Socorro County, New Mexico. 7th Bien. Rept. State Engineer, N. Mex.: 81-87.

Cleaveland, A. M. 1941. No life for a lady. Boston: Houghton Mifflin Co. pp. 288-290.

Clisby, K. H... 1955. Pleistocene climates in New Mexico. Paper given at A.A.A.S. meeting, Atlanta, Georgia, Dec., 1955.

Clisby, K. H. & P. B. Sears. 1955. Palynology in southern North America. Part III: Microfossil profiles under Mexico City correlated with the sedimentary profiles. Geol. Soc. Amer. Bull. **66:** 511-520.

Clisby, K. H. & P. B. Sears. 1956. San Augustin Plains —Pleistocene climatic changes. Science **124**: 537-539.

Cockerill, P. W., B. Hunter & H. B. Pingrey. 1939. Type of farming and ranching areas in New Mexico. Part II. N. Mex. Agr. Expt. Sta. Bull. **267.**

Daubenmire, R. F. 1943. Vegetational zonation in the Rocky Mountains. Bot. Rev. **9:** 325-393.

Dillon, L. S. 1956. Wisconsin climate and life zones in North America. Science **123:** 167-176.

Dortignac, E. J. 1956. Watershed resources and problems of the upper Rio Grande Basin. Rocky Mtn. Forest and Range Expt. Sta., U.S. Forest Serv. (unnumbered)

Emerson, F. W. 1932. The tension zone between the grama grass and pinyon-juniper associations in northeastern New Mexico. Ecology **13:** 347-358.

Foreman, F. 1956. San Augustin Plains—the sediments. Science **124:** 539.

Hitchcock, A. S. 1950. Manual of the grasses of the United States. U.S. Dept. Agr. Misc. Publ. **200:** 2nd ed.

Howell, J. 1941. Pinon and juniper woodlands of the southwest. Jour. Forestry **39:** 542-545.

Kearney, T. H. & R. H. Peebles. 1951. Arizona flora. Univ. Calif. Press, Berkeley, Calif.

Kelting, R. W. 1954. Effects of moderate grazing on the composition and plant production of a native tallgrass prairie in central Oklahoma. Ecology **35:** 200-207.

Kuchler, A. W. 1949. A physiognomic classification of vegetation. Assoc. Amer. Geog. Ann. **39:** 201-210.

———. 1955. A comprehensive method of mapping vegetation. Assoc. Amer. Geog. Ann. **45:** 405-415.

Leopold, Luna B. 1951. Pleistocene climate in New Mexico. Amer. Jour. Sci. **249:** 152-168.

Lindsey, A. A. 1955. Testing the line-strip method against full tallies in diverse forest types. Ecology **36:** 485-495.

Mangelsdorf, P. C. & C. E. Smith, Jr. 1949. New archeological evidence on evolution in maize. Bot. Mus. Leafl. Harvard Univ. **13:** 213-247.

Meinzer, O. E. 1922. Map of the Pleistocene Lakes of the Basin-and-Range Province and its significance. Geol. Soc. Amer. Bull. **33:** 541-552.

Merkle, J. 1952. An analysis of a pinyon-juniper community at Grand Canyon, Arizona. Ecology **33:** 375-384.

Pearson, G. A. 1931. Forest types in the southwest as determined by climate and soil. U.S. Dept. Agr. Tech. Bull. **247.**

Phillips, F. J. 1909. A study of pinon pine. Bot. Gaz. **48:** 216-223.

Powers, W. E. 1939. Basin and shore features of the extinct Lake San Augustin, New Mexico. Jour. Geomorph. **2:** 345-350.

Rice, E. L. & W. T. Penfound. 1954. Plant succession and yield of living plant material in a plowed prairie in central Oklahoma. Ecology **35:** 176-180.

Sears, P. B. & K. H. Clisby. 1955. Palynology in southern North America. Part IV: Pleistocene climate in Mexico. Geol. Soc. Amer. Bull. **66:** 521-530.

Smith, C. E., Jr. 1950. Prehistoric plant remains from Bat Cave. Bot. Mus. Leafl. Harvard Univ. **14:** 157-180.

Springfield, H. W. 1951. Unpublished report on a study of the effects of drought on yield and density of native and reseeded stands at the Monica Site. Rocky Mountain Forest & Range Expert. Sta. Albuquerque, N. M.

Stearns, C. E. 1954. Unpublished map.

———. 1956. San Augustin Plains—the geologic setting. Science **124:** 539.

Thornthwaite, C. W. 1931. The climates of North America according to a new classification. Geog. Rev. **21:** 633-655.

U.S. Dept. Agr. 1938. Soils and Men, Yearbook of Agriculture. U. S. Gov't. Print. Off., Washington, D. C.

———. 1941. Climate and Man, Yearbook of Agriculture. U. S. Gov't. Print. Off., Washington, D. C.

U. S. Weather Bur. 1932. Climatic summary of the United States (through 1930). Sec. 29. Southern New Mexico.

———. 1955. Climatological Data, New Mexico, Summary for 1954.

Voigt, J. W. & J. E. Weaver. 1951 Range condition classes of native midwestern pasture: An ecological analysis. Ecol. Monog. **21:** 39-60.

Watson, J. R. 1912. Plant geography of north-central New Mexico. Bot. Gaz. **54:** 194-217.

Whitfield, C. J. & E. L. Beutner. 1938. Natural vegetation in the desert plains grassland. Ecology **19:** 26-37.

Woodin, H. E. 1953. The pinyon-juniper association in the eastern foothills of the Rockies. Ph.D. thesis, Purdue Univ. (Listed in Dissertation Abstracts.)

Woodin, H. E. & A. A. Lindsey. 1954. Juniper-pinyon east of the continental divide, as analyzed by the line-strip method. Ecology **35:** 473-489.

Woodbury, A. M. 1947. Distribution of pigmy conifers in Utah and northeastern Arizona. Ecology **28:** 113-126.

Wooten, E. O. & P. C. Standley. 1912. Grasses and grass-like plants of New Mexico. N. Mex. Agr. Expt. Sta. Bull. **81.**

OBSERVATIONS ON FLUCTUATIONS OF ACARINE POPULATIONS FROM NESTS OF *PEROMYSCUS LEUCOPUS*

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INTRODUCTION

Nests of small mammals and birds are favorable habitats for many kinds of mites. Bishopp (1923), Sambon (1928), Garman (1937), Linsley (1944), Hughes (1928), Woodruffe & Southgate (1951), Woodruffe (1953) and others have reported that nests are sources of domestic pests and Acarina which are of medical and economic importance.

The acarine fauna of nests of rodents has been studied by several investigators. Oudemans (1913) described many species of mites from moles' nests in Germany. The arthropod inhabitants of the pocket gopher in Texas were studied by Ross (1944). Wharton (1946) collected over 30 species of mites from the general nest area of rats on the island of Guam. Vysotska (1947) collected mites from the nests of *Microtus arvalis* Pallas in Russia. Walters & Roth (1950) collected representatives of 12 families of Acarina from nests of the dusky-footed wood rat. Also from the inner nests of the dusky-footed wood rat Linsdale & Tevis (1951) collected representatives of 14 families of Acarina. Allred & Beck (1953) collected representatives of 43 families of mites from nests of two species of *Neotoma* in Utah.

The method used by most authors to collect mites and other small arthropods from nests is an automatic collecting device such as a Berlese (Berlese 1905) or Tullgren (Tullgren 1917) apparatus. These devices use heat and/or light to drive the arthropods from the nests. A nest is brought in from the field, placed in a funnel, and then a light is suspended above the funnel or hot water is forced through a jacket which surrounds the funnel. The mites are collected in a small vial placed beneath the narrow end of the funnel.

Norberg (1936), in a study of faunal-host relationships of bird nests, used a Tullgren apparatus to collect 272 species of Acarina from nests of 56 species of birds. He also used a different collecting method to find out at what rate arthropods left birds' nests after the nests had been deserted. He enclosed a nest, as it was in the field, in a sack of cheesecloth which had a flask attached to the bottom. Any arthropods leaving the nest would be captured in the liquid in the flask. By exchanging flasks at intervals of ten days, Norberg was able to determine the dynamic aspect of the arthropods' leaving the abandoned birds' nests.

The effect of climatic conditions and nesting activity of the wood mouse, *Peromyscus leucopus noveboracensis* (Fischer), upon the fluctuations in numbers and kinds of Acarina escaping from the nests of this small mammal is considered here. In order to do this it was necessary to devise a new technique for collecting nidicoles without disturbing the nest. Previous studies of the fluctuations of the ectoparasites in the nests of rodents were not made on the same nests over a period of time. Therefore, the effect of variation from nest to nest was introduced into the data. As a result, the data obtained here are not strictly comparable to other similar studies. The predicament of investigators using techniques that involve the destruction of nests is emphasized by Linsdale & Tevis (1951) as follows: "The kinds of invertebrates to be found within occupied rat houses and the numerical proportions between kinds depends on many other factors than the season of the year and the location, for adjacent houses examined at the same time differ markedly in their invertebrate fauna."

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Huber, for making the collecting trips in the author's absence and Dr. and Mrs. W. H. Stickel, Patuxent Research Refuge, for valuable advice regarding the field work. The field work was done at the Patuxent Wildlife Research Refuge, Bowie, Maryland, with the cooperation of the Fish and Wildlife Service, United States Department of Interior. This investigation was supported by the Medical Research and Development Board, Office of the Surgeon General, Department of the Army, under Contract No. DA-49-007-MD-501.

MATERIALS AND METHODS

Nest-boxes have been used successfully to study the habits and life history of the wood mouse. Nicholson (1941) used them in his investigations of *Peromyscus leucopus noveboracensis* in southern Michigan, as did Jackson (1953) in a study of the same subspecies in New Jersey. The wooden nest-boxes were used by the mice as nesting sites and feeding stations. Nest-boxes were modified for this study so that mites could be collected from the nests. The floor of the typical nest-box was changed from wood to ⅛-inch hardware cloth beneath which was attached a funnel. A bottle cap was soldered to the narrow end of the funnel; this cap had a hole in it through which the end of the funnel protruded. Bottles which contained water or a weak solution of ethyl alcohol were screwed into the bottle cap. Thus any mites leaving the nest were captured in the liquid in the bottle. This collecting apparatus (Fig. 1) is called the nest-funnel (Drummond 1955).

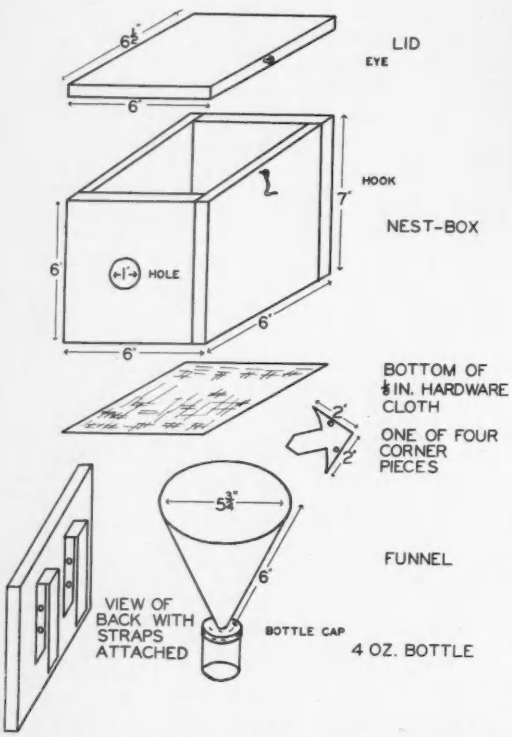

FIG. 1. Exploded view of a nest-funnel with a view of back showing straps for attachment.

Nest-funnels were attached to trees in the field (Fig. 2) by means of two metal straps screwed into the back of the box. One arm of these inverted U-shaped straps was screwed to the nest-funnel and the other was slipped over a block of wood which was nailed to a tree.

FIG. 2. Nest-funnel in position in the study area.

The trees were located in the Patuxent Research Refuge of the Fish and Wildlife Service, United States Department of Interior (Fig. 3). The study area, consisting of 27.5 acres, is located on a terrace near the Patuxent River and includes the edges of woods and several hedge rows surrounding two small fields of lespedeza (Fig.4).

Nest-funnels were placed in the study area at 5 intervals during a 20-month period. The first group of 12, placed in the field on October 12, 1953, had mice and nesting material from occupied *P. leucopus noveboracensis* nests dumped into them. The second, third, fourth, and fifth groups were placed in the field at various times from December 9, 1953, to December 8, 1954. The 20 nest-funnels of these latter groups contained only sterilized straw and no attempt was made to "seed" them. All nest-funnels were placed at convenient heights on trees so that they were evenly spaced throughout the study area and were easy to examine. Besides the nest-funnels another

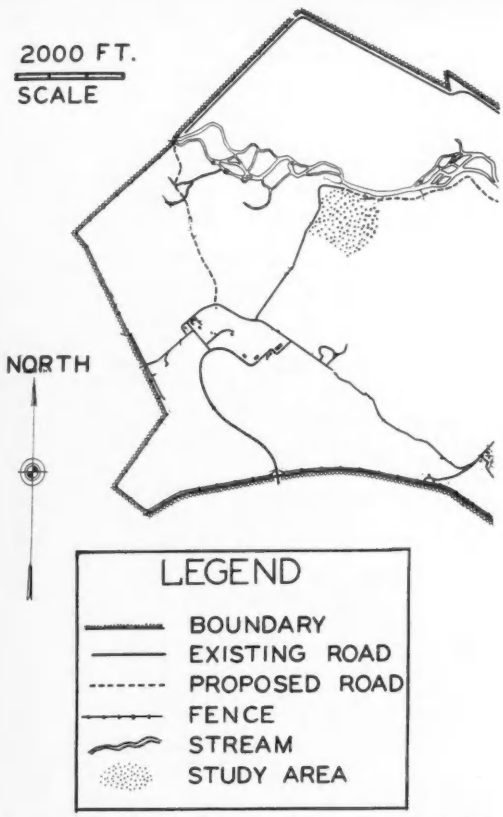

FIG. 3. Northwest portion of Patuxent Research Refuge, Bowie, Maryland, showing location of study area.

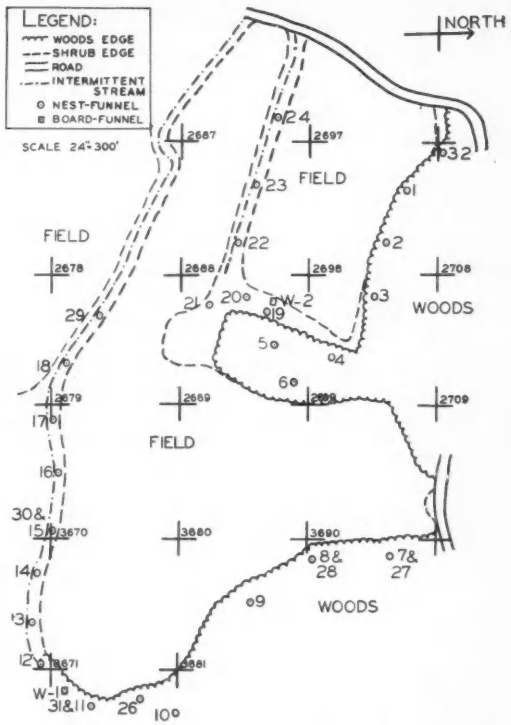

FIG. 4. Study area showing locations of nest-funnels.

type of funnel, the board-funnel, was placed in the field. The board-funnel (Fig. 5) was similar to the nest-funnel except that a board replaced the nest-box and was not touching the funnel. The open end of the funnel was exposed to the environment under the board; mice could not enter this environment. Two of these board-funnels were constructed and placed in the field area on November 24, 1954.

Near the end of the study period, six more nest-funnels were placed in the area. These nest-funnels were similar to those already in the field except that each contained two adult *Peromyscus leucopus noveboracensis*. These mice were raised in the laboratory and had no opportunity to pick up mites from the field. They were provided with sterile straw with which they could construct their nests, but they could not escape from the nest-funnels because pieces of ¼-inch hardware cloth were nailed over the openings and the lids were securely fastened by hooks and eyes. Food and water were supplied for the mice. These nest-funnels were placed on trees in the field on October 5, 1955, and removed on November 9, 1955. These nest-funnels were visited twice each week.

The nest-funnels were visited on 96 Wednesdays from January 1, 1954, through November 2, 1955. During these weekly visits, three operations were performed: (1) nest-funnels were inspected for mice, or nesting activity of mice, (2) bottles which had been attached to the funnels were replaced by other bottles, and (3) maximum and minimum air temperatures for the week were recorded.

The mites which had been collected in the bottles were then sorted and identified. The number of mites collected from any one funnel per week rarely exceeded 50 specimens or 7 species so that with the aid of a dissecting microscope the mites could be grouped into "similar types." By this method, most mites could be grouped according to family or genus. Then a slide was made of a representative of each group to insure proper identification. After slides had been made, the remaining mites were placed in 70% alcohol in tubes which were labeled with the date and nest number. The identification and number of each type was checked twice during the study period. The data consisted of collections of Acarina about which the following were known: number of nest-funnel, date of collection, nesting information, temperature, and number and kinds of Acarina.

The fluctuations in numbers and kinds of Acarina escaping from the nests were correlated with two factors of the environment. The first factor was the nesting activity of the mice. The collections were divided into four groups on the basis of nesting

TABLE 1. Weekly average air temperatures in degrees Fahrenheit by season from the weather station at Ft. Meade, Maryland, and study area at Patuxent Research Refuge.

Winter, 1954	January	February			
Date	6 13 20 27	3 10			
Ft. Meade Average	37 30 30 39	37 35° F.			
Early Spring, 1954	Feb.	March	April		
Date	17 24	3 10 17 24 30	7 14		
Ft. Meade Average	47 43	45 39 39 44 52	47 56° F.		
Late Spring, 1954	April	May	June		
Date	21 28	5 12 19 26	2 9		
Ft. Meade Average	62 65	62 52 58 61	71 66° F.		
Summer, 1954	June	July	August	September	Oct.
Date	16 23 30	7 14 21 28	4 11 18 25	1 8 15 22 29	6
Ft. Meade Average	75 70 73	76 79 75 73	80 71 70 73	72 75 68 69 64	75° F.
Fall, 1954	October	November			
Date	13 20 27	3 10 17 24			
Ft. Meade Average	62 56 54	42 40 44 49° F.			
Study Area	59 48	43 40 41 44° F.			
Winter, 1954-5	December	January	February		
Date	1 8 15 22 29	5 12 19 26	2 9 16		
Ft. Meade Average	38 30 37 32 40	43 35 32 30	23 29 31° F.		
Study Area	37 30 30 32 37	40 32 27 23	19 23 29° F.		
Early Spring, 1955	Feb.	March	April		
Date	23	2 9 16 23 30	6 13		
Ft. Meade Average	41	46 42 55 45 40	51 54° F.		
Study Area	36	41 41 52	.. ..° F.		
Late Spring, 1955	April	May	June		
Date	20 27	4 11 18 25	1 8 15		
Ft. Meade Average	60 59	58 63 60 69	70 66 62° F.		
Study Area	.. ..	.. ..	.. .. ..		
Summer, 1955	June	July	August	September	
Date	22 29	6 13 20 27	3 10 17 24 31	7 14 21	
Ft. Meade Average	72 69	79 78 80 81	80 78 76 77 73	72 64 71° F.	
Study Area	67 66	72 68 70 76	79 x 75 72 72	72 61 64° F.	
Fall, 1955	Sept.	October	Nov.		
Date	28	5 13 19 25	2		
Ft. Meade Average	62	62 63 59 52	54° F.		
Study Area	58	60 61 58 53	47° F.		

..Thermometer broken.
xThermometer out of adjustment.

activity. The first group, "never observed occupied," consisted of those collections from nest-funnels in which neither mice nor nesting material other than sterile straw had been observed. The second group, "observed occupied," was composed of those collections from nest-funnels in which mice were observed during the collecting trips. The third group, "unoccupied 1-4 weeks," was made up of collections from nest-funnels during the one to four weeks period following the last week in which mice were observed in the nest-funnels. The fourth group, "abandoned," was defined as collections from nest-funnels after the unoccupied one to four weeks period until the next observed occupied period.

The second factor of the environment was the seasonal climatic conditions of the general area of the study as determined by the mean air temperature. The climatological data were obtained from weekly maximum-minimum temperatures of the study area. Daily maxima and minima recorded at the Ft. Meade Weather Station were used to divide the years into seasons based on temperature (Table 1). Series of

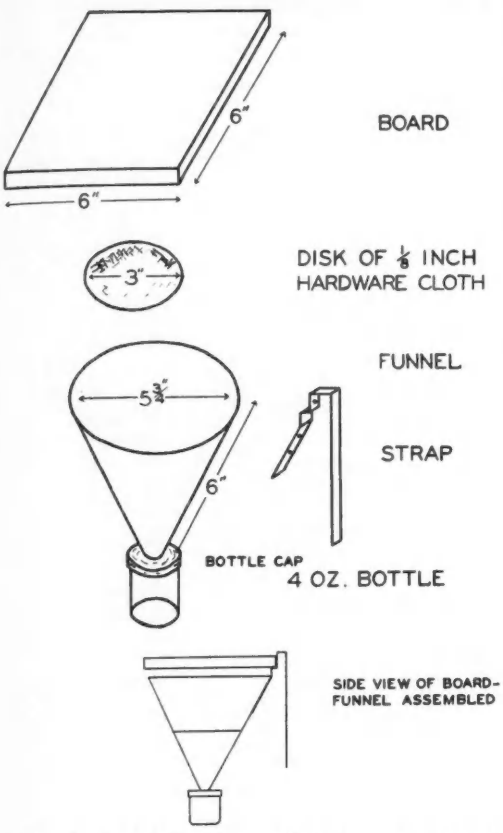

FIG. 5. Exploded and assembled views of a board-funnel.

weeks which had similar mean temperatures; *i.e.*, average of all daily maxima and minima, were placed together as a season and where there was a large difference between the mean temperature of two consecutive weeks, the division between two seasons was placed. By this method the year was divided into 5 seasons: winter, average temperature 33° F; early spring, average temperature 46° F; late spring, average temperature 62° F; summer, average temperature 74° F; and fall, average temperature 54° F.

In order to determine and compare the effect of these two factors upon the numbers and kinds of Acarina escaping from the nests, certain statistical procedures were used. Analysis of variance, commonly used in quantitative and qualitative analysis, was not applicable because the distribution of observed fluctuations was not normal but contagious (Cole & Koepke 1947). In order to determine whether or not the observed fluctuations in numbers and kinds of Acarina could be explained by chance alone, or could be attributed to differences in seasonal climatic conditions or nesting activity, a chi-square method of analysis was used.

An R x C table for test of independence (Snedecor

TABLE 2. List of species of Acarina collected from nest-funnels classified according to dietary habits and mode of entry into nest-funnels.

Species	Dietary Habit			Mode of Entry			
	Parasit.	Pred.	Misc.	Actively	On Mice	Nest. Mat.	Undet.
SUBORDER MESOSTIGMATA							
COHORT GAMASINA							
Ascaidae							
1 *Asca* sp. A	..	X	..	..	..	X	..
2 *Asca* sp. B	..	X	..	..	..	X	..
3 *Asca* sp. C	..	X	..	..	..	X	..
4 *Gamasellus* sp. A	..	X	..	..	..	X	..
Parasitidae							
5 *Parasitus* sp. A	..	X	..	..	X	..	..
Macrochelidae							
6 *Macrocheles* sp. A	..	X	..	..	..	X	..
Pachylaelaptidae							
7 Species A	..	X	..	..	..	..	X
8 *Pachylaelaps* sp. B	..	X	..	..	..	X	..
Haemogamasidae							
9 *Haemogamasus liponyssoides* Ewing, 1925	X	..	..	..	X	..	..
Dermanyssidae							
10 *Ornithonyssus bacoti* (Hirst, 1913)	X	..	..	..	X	..	..
11 *Ornithonyssus bursa* (Berlese, 1888)	X	..	..	..	..	..	X
12 *Ornithonyssus* sp. A	X	..	..	..	X	..	..
13 *Dermanyssus gallinae* (DeGeer, 1778)	X	..	..	..	..	..	X
Phytoseiidae							
14 *Amblyseius americanus* Garman, 1948	..	X	..	X	..	..	..
15 *Amblyseius grandis* Berlese, 1914	..	X	..	..	X	..	..
16 *Amblyseius* sp. A	..	X	..	..	..	X	..
17 *Amblyseius* sp. B	..	X	..	..	..	..	X
18 *Ameroseius* sp. A	..	X	..	..	..	X	..
19 *Blattisocius tineivorus* (Oudemans, 1929)	..	X	..	..	..	X	..
20 *Garmania bulbicola* (Oudemans, 1929)	..	X	..	..	X	..	..
21 *Garmania* sp. A	..	X	..	..	..	..	X
22 *Garmania* sp. B	..	X	..	..	..	..	X
23 *Garmania* sp. C	..	X	..	..	..	..	X
24 *Lasioseius* sp. A	..	X	..	..	..	X	..
25 *Phytoseius macropilus* (Banks, 1909)	..	X	..	..	..	X	..
26 *Podocinum* sp. A	..	X	..	..	..	X	..
27 *Typhlodromus* sp. A	..	X	..	..	X	..	..
28 *Typhlodromus* sp. B	..	X	..	..	..	X	..
29 *Typhlodromus* sp. C	..	X	..	..	..	X	..
30 *Zercoseius* sp. A	..	X	..	..	X	..	..
31 *Zercoseius* sp. B	..	X	..	..	X	..	..
Laelaptidae							
32 *Androlaelaps* sp. A	..	X	..	..	..	..	X
33 *Androlaelaps* sp. B	..	X	..	..	..	..	X
34 *Cosmolaelaps* sp. A	..	X	..	..	X	..	..
35 *Cosmolaelaps* sp. B	..	X	..	..	..	X	..
36 *Eulaelaps stabularis* (Koch, 1836)	X	..	..	..	..	X	..
37 *Eviphis* sp. A	..	X	..	..	..	X	..
38 *Gymnolaelaps* sp. A	..	X	..	..	X	..	..
39 *Haemolaelaps glasgowi* (Ewing, 1925)	X	..	..	..	X	..	..
40 *Haemolaelaps megaventralis* (Strandt., 1947)	X	..	..	..	X	..	..
41 *Hypoaspis* sp. A	..	X	..	..	..	X	..
42 *Hypoaspis* sp. B	..	X	..	..	..	X	..
43 *Laelaspis* sp. A	..	X	..	..	..	X	..
44 *Laelaptoid* nymph	..	X	..	..	X	..	..
Zerconidae							
45 *Zercon* sp. A	..	..	X	..	..	X	..
COHORT UROPODINA							
Trachytidae							
46 *Polyaspinus* sp. A	..	..	X	..	..	X	..
Uropodidae							
47 *Oplitis* sp. A	..	..	X	..	X	..	..
SUBORDER IXODES							
Ixodidae							
48 *Ixodes dentatus* Marx, 1899	X	..	..	..	X	..	..
49 *Dermacentor variabilis* (Say, 1821)	X	..	..	..	X	..	..

TABLE 2, Continued

Species	Dietary Habit: Parasit.	Pred.	Misc.	Mode of Entry: Actively	On Mice	Nest. Mat.	Undet.
SUBORDER TROMBIDIFORMES							
COHORT TARSONEMINA							
Scutacaridae							
50 *Scutacarus* sp. A	..	..	X	X	..	..	..
51 *Scutacarus* sp. B	..	..	X	..	X	..	..
52 *Scutacarus* sp. C	..	..	X	..	..	..	X
Pyemotidae							
53 *Resinacarus* sp. A	..	..	X	..	X	..	..
COHORT PROMATINA							
Eupodidae							
54 *Eupodes* sp. A	..	..	X	..	X	..	..
55 *Cocceupodes* sp. A	..	..	X	..	X	..	..
56 *Penthaelus minor* (Canestrini, 1886)	..	..	X	..	..	X	..
Bdellidae							
57 *Bdella* sp. A	..	X	..	..	..	..	X
58 *Bdella oblonga* Say, 1821	..	X	..	X	..	..	..
59 *Bdella recens* Ewing, 1937	..	X	..	..	..	X	..
60 *Bdella willisi* Baker, 1944	..	X	..	..	..	X	..
61 *Biscirus silvaticus* (Kramer, 1881)	..	X	..	..	X	..	..
62 *Biscirus* sp. A	..	X	..	..	X	..	..
63 *Spinibdella depressa* (Ewing, 1909)	..	X	..	..	..	X	..
64 *Cyta latirostris* (Hermann, 1804)	..	X	..	..	..	X	..
Rhagidiidae							
65 *Rhagidia* sp. A	..	X	..	..	..	X	..
66 *Rhagidia* sp. B	..	X	..	..	X	..	..
67 *Rhagidia* sp. C	..	X	..	..	X	..	..
68 *Rhagidia* sp. D	..	X	..	..	..	..	X
69 *Rhagidia* sp. E	..	X	..	..	..	..	X
70 *Rhagidia* sp. F	..	X	..	..	..	X	..
Ereynetidae							
71 Species A	..	..	X	..	..	..	X
Tydeidae							
72 *Tydeus* sp. A	..	X	..	..	X	..	..
73 *Tydeus* sp. B	..	X	..	..	..	..	X
74 *Tydeus* sp. C	..	X	..	..	..	X	..
75 *Tydeus* sp. D	..	X	..	..	..	..	X
76 *Lorryia* sp. A	..	X	..	..	..	..	X
77 *Pronematus* sp. A	..	X	..	..	..	..	X
Cunaxidae							
78 *Cunaxa mexicana* Baker and Hoffman, 1948	..	X	..	..	..	..	X
79 *Cunaxa* sp. A	..	X	..	..	..	X	..
80 *Cunaxa* sp. B	..	X	..	..	..	X	..
81 *Cunaxa* sp. C	..	X	..	..	..	..	X
82 *Cunaxoides* sp. A	..	X	..	..	..	X	..
Raphignathidae							
83 *Raphignathus* sp. A	..	X	..	..	..	..	X
84 *Raphignathus* sp. B	..	X	..	..	..	..	X
85 *Raphignathus* sp. C	..	X	..	..	..	X	..
Caligonellidae							
86 Species A	..	X	..	..	X	..	..
87 Species B	..	X	..	..	..	X	..
88 *Neophyllobius* sp. A	..	X	..	..	..	..	X
Stigmaeidae							
89 *Ledermulleria* sp. A	..	X	..	..	X	..	..
90 *Ledermulleria* sp. B	..	X	..	..	..	..	X
91 *Ledermulleria* sp. C	..	X	..	..	X	..	..
92 *Ledermulleria* sp. D	..	X	..	..	..	..	X
Tetranychidae							
93 *Tetranychus telarius* group	..	..	X	..	..	..	X
94 *Bryobia praetiosa* Koch, 1836	..	..	X	..	X	..	..
Phytoptipalpidae							
95 *Pentamerismus* sp. A	..	..	X	..	..	..	X
Anystidae							
96 *Anystis* sp. A	..	X	..	..	X	..	..
Cheyletidae							
97 *Cheyletus eruditus* Shrank, 1781	..	X	..	..	X	..	..
98 *Cheyletomorpha lepidopterorum* Shaw, 1794	..	X	..	..	X	..	..

TABLE 2, Continued

Species	Dietary Habit: Parasit.	Pred.	Misc.	Mode of Entry: Actively	On Mice	Nest. Mat.	Undet.
COHORT PARASITENGINA							
Erythraeidae							
99 *Balaustium* sp. A	..	X	..	..	X	..	..
100 *Balaustium* sp. B	..	X	..	..	X	..	..
101 *Leptus* sp. A	..	X	..	..	..	X	..
102 *Leptus* sp. B	..	X	..	..	..	X	..
103 *Leptus* sp. C	..	X	..	..	..	X	..
104 *Sphaerolophus* sp. A	..	X	..	..	X	..	..
105 Larvae sp. A	..	X	..	..	..	X	..
106 Larvae sp. B	..	X	..	..	..	X	..
107 Larvae sp. C	..	X	..	..	..	..	X
Smaridiidae							
108 Adult sp. A	..	X	..	..	..	X	..
109 Larvae sp. A	..	X	..	..	..	X	..
110 *Hauptmannia* sp. A	..	X	..	..	X	..	..
Trombidiidae							
111 *Podothrombium* sp. A	..	X	..	X	..	..	..
Trombiculidae							
112 *Trombicula jonesae* Brennan, 1952	X	..	..	..	..	X	..
113 *Trombicula whartoni* Ewing, 1926	X	..	..	..	X	..	..
114 *Trombicula* sp. B	X	..	..	..	..	..	X
115 *Trombicula* sp. C	X	..	..	..	..	X	..
116 *Euschöngastia peromyci* (Ewing, 1929)	X	..	..	..	..	X	..
117 *Euschöngastia setosa* Ewing, 1937	X	..	..	..	X	..	..
118 *Walchia americana* Ewing, 1942	X	..	..	..	..	X	..
COHORT ENDEOSTIGMATINA							
Lordalychidae							
119 *Lordalychus* sp. A	..	..	X	..	..	..	X
Terpnacaridae							
120 Species A	..	..	X	..	..	..	X
121 Species B	..	..	X	..	..	X	..
SUBORDER SARCOPTIFORMES							
COHORT ACARIDIA							
Acaridae							
122 *Aleuroglyphus* sp. A	..	..	X	..	..	..	X
123 *Caloglyphus* sp. A	..	..	X	..	..	X	..
124 *Caloglyphus* sp. B	..	..	X	..	..	..	X
125 *Eberhardia* sp. A	..	..	X	..	..	X	..
126 *Rhizoglyphus* sp. A	..	..	X	..	X	..	..
127 *Rhizoglyphus* sp. B	..	..	X	..	..	..	X
128 *Suidasia* sp. A	..	..	X	..	..	X	..
129 *Thyreophagus entomophagus* (Laboulbene, 1852)	..	..	X	..	..	X	..
130 *Tyrophagus* sp. A	..	..	X	..	X	..	..
131 *Tyrophagus* sp. B	..	..	X	..	..	X	..
132 *Tyrophagus lintneri* (Osborne, 1893)	..	..	X	..	X	..	..
Glycyphagidae							
133 *Dermacarus* sp. A	..	..	X	..	X	..	..
134 *Dermacarus* sp. B	..	..	X	..	..	..	X
135 *Fuscherica* sp. A	..	..	X	..	..	..	X
136 *Labidophorus* sp. A	..	..	X	..	X	..	..
137 *Labidophorus sciurinus* (Koch, 1841)	..	..	X	..	..	..	X
Anoetidae							
138 *Histiostoma* sp. A	..	..	X	..	..	X	..
139 *Histiostoma* sp. B	..	..	X	..	..	..	X
140 *Histiostoma* sp. C	..	..	X	..	..	X	..
COHORT PSOROPTIDIA							
Listrophoridae							
141 *Myocoptes* sp. A	X	..	..	..	..	X	..

1945) was applied to the data and was used to analyze the effects of the seasonal climatic conditions and nesting activity of the mice upon: (1) relative frequency of kinds of mites according to feeding habits, (2) number of species per collection, (3) total mites per collection, (4) number of *Haemolae-*

laps glasgowi (Ewing), a parasite of the mice, per collection, (5) number of *Dermacentor variabilis* (Say), the American dog tick, per collection and (6) the effects of the two factors, season and nesting activity, on each other.

RESULTS

The Acarina were identified and, when possible, grouped into species. There were 141 species distributed in 74 genera, 37 families, and 4 suborders (Table 2). The genus of most species was determined when the mites were collected. All members of a genus were examined together and the different types were designated as species "A," "B," *etc.* Since it was impossible to determine the species or genus of all mites, not all were included in the list of species. If larval and nymphal stages, hypopial Acaridiae, and the Oribatei had been identified to species, the faunal list would have included at least 35 more species. The mites were classified according to the system presented by Baker & Wharton (1952) as modified by their students: Camin & Gorirossi (1955), Mesostigmata; Cunliffe (1955), Trombidiformes; and Yunker (1955), Sarcoptiformes.

The species of mites were divided into three groups on the basis of general feeding habits. These groups were: (1) parasitic, those mites which are parasitic on mice or other vertebrates; (2) predaceous, those mites which prey on mites and small arthropods; and (3) miscellaneous, mites which are phytophagous, fungivorous, saprophagous, or have any dietary habit other than parasitic or predaceous. The different kinds of mites were placed in their respective dietary groups according to information given by Baker & Wharton (1952). Although each species of mite had a characteristic seasonal pattern of occurrence, the relative proportions of kinds of parasites, predators and miscellaneous feeders did not change with nesting activity or season (Tables 3 and 4).

In contrast to collections from nest-funnels, there were only four species in the collections from the board-funnels. Three species, *Amblyseius americanus, Bdella oblonga, Podothrombium* sp. A, were in the predaceous group and one species, *Scutacarus* sp. A, was in the miscellaneous feeding group.

Six special nest-funnels were in the field for five weeks. During this period three of these had to be discarded because mice had chewed their way out of the nest-funnels. There were three predaceous species, *Macrocheles* sp. A, *Hypoaspis* sp. A, *Garmania* sp. C, in 22 collections from these nest-funnels.

During the study period, 17,201 mites were collected from the nest-funnels. Of this number 4,983 (29.0%) were parasitic including 1,748 *H. glasgowi*, 3,638 (21.1%) were predaceous, 6,166 (35.9%) had miscellaneous feeding habits and 2,414 (14.0%) could not be placed into any of the three dietary groups. There were also 244 *D. variabilis* (175 larvae, 66 nymphs, 3 adults) and 5 *Ixodes texanus* collected.

Considerable variation in the kinds of mites and the numbers of mites collected from each nest-funnel was noted (Table 5). The observed numbers and kinds of mites from any one nest-funnel were not necessarily indicative of the numbers and kinds col-

TABLE 3. Numbers of species of mites in three dietary groups classified according to nesting activity.

Nesting Activity		Dietary Groups			Total Species
		Parasitic	Predaceous	Miscellaneous	
Observed Occupied	Expected	8.3	39.3	13.4	61
	Observed	11.0	40.0	10.0	
	Deviation	2.7	.7	−3.4	
Unoccupied 1-4 Weeks	Expected	10.1	47.7	16.2	
	Observed	10.0	47.0	17.0	74
	Deviation	−.1	− .7	.8	
Abandoned	Expected	14.6	69.6	23.8	
	Observed	13.0	70.0	25.0	108
	Deviation	−1.6	.4	1.2	
Never Observed Occupied	Expected	6.0	28.4	9.6	
	Observed	5.0	28.0	11.0	44
	Deviation	−1.0	−.4	1.4	
Total		39	185	63	287

Chi-square: 2.43
Degrees of freedom: 6
Probability: .9-.8 Differences not statistically significant.

TABLE 4. Numbers of species of mites in three dietary groups classified according to season.

Season		Dietary Groups			Total Species
		Parasitic	Predaceous	Miscellaneous	
Winter	Expected	7.4	27.4	11.2	
	Observed	10.0	22.0	14.0	46
	Deviation	2.6	−5.4	2.8	
Early Spring	Expected	10.3	38.1	15.6	
	Observed	11.0	34.0	19.0	64
	Deviation	.7	−4.1	3.4	
Late Spring	Expected	10.0	37.5	15.5	
	Observed	8.0	44.0	11.0	63
	Deviation	−2.0	6.5	−4.5	
Summer	Expected	10.3	38.1	15.6	
	Observed	9.0	39.0	16.0	64
	Deviation	−1.3	.9	.4	
Fall	Expected	8.0	29.9	12.1	
	Observed	8.0	32.0	10.0	50
	Deviation	0	2.1	−2.1	
Total		46	171	70	287

Chi-square: 6.44
Degrees of freedom: 8
Probability: .7-.5 Differences not statistically significant.

TABLE 5. Total number and dietary habits of all mites collected from the nest-funnels.

Nest-funnel Number	Parasitic		Predaceous	Miscellaneous	Undetermined	Total Mites
	Haemolaelaps[1] *glasgowi*	Total				
1	27	242	173	615	51	1,081
2	181	514	173	256	101	1,044
3	162	364	162	219	418	1,163
4	31	67	58	67	36	228
5	111	436	285	228	350	1,299
6	35	96	124	140	17	377
7	8	25	36	151	7	219
8	20	49	35	40	17	141
9	131	297	123	373	171	964
10	10	14	23	8	1	46
11	9	11	46	64	5	126
12	60	96	97	43	38	274
13	24	64	84	227	28	403
14	29	132	353	369	20	874
15	7	31	21	64	13	129
16	117	171	174	190	126	661
17	10	26	122	40	6	194
18	25	105	249	778	88	1,220
19	59	154	215	352	199	920
20	32	150	138	129	62	479
21	148	521	100	538	77	1,236
22	48	62	57	71	12	202
23	27	67	67	31	19	184
24	11	40	74	27	17	158
25	12	64	123	404	21	612
26	98	426	90	89	173	778
27	23	55	27	22	6	110
28	162	457	118	518	151	1,244
29	61	95	58	18	98	269
30	21	67	81	61	49	258
31	0	0	62	14	0	76
32	49	85	90	20	37	232
Totals....	1,748	4,983	3,638	6,166	2,414	17,201

[1]The number of mites in the *Haemolaelaps glasgowi* column is included in the total parasitic column.

lected from what might be called a comparable funnel. Nevertheless, when the collections from all nest-funnels were lumped together according to certain environmental attributes, an interpretable pattern emerged. The significance of these patterns was demonstrated by a series of R x C tests.

The first set of R x C tests had as the constant attribute the total number of species of mites per collection. The collections were placed into 4 groups: 0, 1-2, 3-4, and 5 or more species of mites per collection. The second attribute of the collections in the first test of this set was the nesting activity of the mice in the nest-funnels on the day of the collections (Table 6). The hypothesis that the number of species per collection was independent of the nesting activity of the mice was rejected because the total chi-square exceeded the .01 level of confidence. The season of the collections was the second attribute of the last test of this set (Table 7). The hypothesis that the number of species per collection was independent of the season of the collection was rejected because the total chi-square exceeded the .01 level of confidence.

TABLE 6. Numbers of collections in four groups of total species of mites per collection classified according to nesting activity.

Nesting Activity		Number of Species				Total Collections
		0	1 - 2	3 - 4	5 or more	
Observed Occupied	Expected	115*	108	34*	18*	
	Observed	29	85	85	76	275
	Deviation	−86	−23	51	58	
Unoccupied 1 - 4 Weeks	Expected	177*	167	52*	27	
	Observed	120	189	80	34	423
	Deviation	−57	22	28	7	
Abandoned	Expected	471*	444	138*	74*	
	Observed	551	459	90	27	1127
	Deviation	80	15	−48	−47	
Never Observed Occupied	Expected	141*	134	42*	22*	
	Observed	204	120	11	4	339
	Deviation	63	−14	−31	−18	
Total Collections		904	853	266	141	2164

Chi-square: 498.60**
Degrees of freedom: 9
*Chi-square exceeds .01 level of confidence for one degree of freedom.
**Highly significant.

TABLE 7. Numbers of collections in four groups of total species of mites per collection classified according to the season.

Season		Number of Species				Total Collections
		0	1 - 2	3 - 4	5 or more	
Winter	Expected	178	168	52	29	
	Observed	197	154	48	28	427
	Deviation	19	−14	−4	−1	
Early Spring	Expected	166*	156	49*	25*	
	Observed	94	153	91	58	396
	Deviation	−72	−3	42	33	
Late Spring	Expected	166	156	49	26	
	Observed	141	178	56	22	397
	Deviation	−25	22	7	−4	
Summer	Expected	281*	267	83*	43*	
	Observed	356	273	38	7	674
	Deviation	75	6	−45	−36	
Fall	Expected	113	106	33	18	
	Observed	116	95	33	26	270
	Deviation	3	−11	0	8	
Total Collections		904	853	266	141	2164

Chi-square: 192.68**
Degrees of freedom: 12
*Chi-square exceeds .01 level of confidence for one degree of freedom.
**Highly significant.

TABLE 8. Numbers of collections in five groups of total mites per collection classified according to nesting activity.

Nesting Activity		Total Mites Per Collection					Total Collections
		0	1 - 5	6 - 25	26 - 100	101 or more	
Observed Occupied	Expected	95*	111*	49*	15*	5*	
	Observed	20	72	106	54	23	275
	Deviation	−75	−39	57	39	18	
Unoccupied 1 - 4 Weeks	Expected	148*	170	76*	22	7	
	Observed	92	176	118	29	8	423
	Deviation	−56	6	42	7	1	
Abandoned	Expected	394*	453	201*	60*	19*	
	Observed	459	490	144	28	6	1127
	Deviation	65	37	−57	−32	−13	
Never Observed Occupied	Expected	119*	136	60*	18*	6*	
	Observed	185	132	18	4	0	339
	Deviation	68	−4	−42	−14	−6	
Total Collections		756	870	386	115	37	2164

Chi-square: 492.67**
Degrees of freedom: 12
*Chi-square exceeds .01 level of confidence for one degree of freedom.
**Highly significant.

TABLE 9. Numbers of collections in five groups of total mites per collection classified according to season.

Season		Total Mites Per Collection					Total Collections
		0	1 - 5	6 - 25	26 - 100	101 or more	
Winter	Expected	149*	172	76	23	7	
	Observed	181	150	64	28	4	427
	Deviation	32	−22	−12	5	−3	
Early Spring	Expected	138*	159	71*	21*	7*	
	Observed	82	150	112	36	16	396
	Deviation	−56	−9	41	15	9	
Late Spring	Expected	139*	160*	71	20	7	
	Observed	108	188	84	16	1	397
	Deviation	−31	28	13	−4	−6	
Summer	Expected	236*	271	120*	36*	11	
	Observed	288	283	84	15	4	674
	Deviation	52	12	−36	−21	−7	
Fall	Expected	94	108	48	15	5*	
	Observed	97	99	42	20	12	270
	Deviation	3	−9	−6	5	7	
Total Collections		756	870	386	115	37	2164

Chi-square: 157.66**
Degrees of freedom: 16
*Chi-square exceeds .01 level of confidence for one degree of freedom.
**Highly significant.

The second set of R x C chi-square tests had as the constant attribute the total mites per collection which were grouped into 0, 1-5, 6-25, 26-100, and 101 or more mites per collection. The first test involved total mites and nesting activity of the mice (Table 8). The hypothesis that total number of mites per collection was independent of nesting activity of the mice was rejected because the total chi-square exceeded the .01 level of confidence. The second test of this set involved total mites per collection and season of the collections (Table 9). The hypothesis that total mites per collection was independent of the season was rejected because total chi-square exceeded the .01 level of confidence.

The third set of R x C chi-square tests had as the constant attribute the number of *H. glasgowi* per collection. The collections were placed in four groups: 0, 1-2, 3-5, 6 or more *H. glasgowi* per collection. The first test involved *H. glasgowi* per collection and nesting activity of the mice (Table 10). The hypothesis that the number of *H. glasgowi* per collection was independent of the nesting activity of the mice was rejected because the total chi-square exceeded .01 level of confidence. The second attribute of the last test of this set was the season of the collection (Table 11). The hypothesis that the number of *H. glasgowi* per collection was independent of the season of the collection was rejected because the total chi-square exceeded the .01 level of confidence.

The fourth set of R x C tests had as the constant attribute the number of *Dermacentor variabilis* per collection. The collections were placed in three

TABLE 10. Numbers of collections in four groups of total *Haemolaelaps glasgowi* per collection classified according to nesting activity.

Nesting Activity		Total *Haemolaelaps glasgowi* per collection				Total Collections
		0	1 - 2	3 - 5	6 or more	
Observed Occupied	Expected	220*	37*	10*	8*	
	Observed	163	59	29	24	275
	Deviation	−57	22	19	16	
Unoccupied 1 - 4 Weeks	Expected	339*	57*	15*	12*	
	Observed	282	87	31	23	423
	Deviation	−57	30	16	11	
Abandoned	Expected	902*	151*	40*	34*	
	Observed	981	120	14	12	1127
	Deviation	79	−31	−26	−22	
Never Observed Occupied	Expected	272	45*	12*	10	
	Observed	307	24	3	5	339
	Deviation	35	−21	−9	−5	
Total Collections		1733	290	77	64	2164

Chi-square: 216.43**
Degrees of freedom: 9
*Chi-square exceeds .01 level of confidence for one degree of freedom.
**Highly significant.

TABLE 11. Numbers of collections in four groups of total *Haemolaelaps glasgowi* per collection classified according to season.

Season		Total *Haemolaelaps glasgowi* per collection				Total Collections
		0	1 - 2	3 - 5	6 or more	
Winter	Expected	342	57	15	13	427
	Observed	364	41	14	8	
	Deviation	22	−16	−1	−5	
Early Spring	Expected	317*	54*	14*	11	396
	Observed	265	87	26	18	
	Deviation	−52	33	12	7	
Late Spring	Expected	318	53*	14	12	397
	Observed	281	80	23	13	
	Deviation	−37	27	9	1	
Summer	Expected	540*	90*	24*	20*	674
	Observed	617	51	5	1	
	Deviation	77	−39	−19	−19	
Fall	Expected	216	36	10	8*	270
	Observed	206	31	9	24	
	Deviation	−10	−5	−1	16	
Total Collections		1733	290	77	64	2164

Chi-square: 170.45**
Degrees of freedom: 12
*Chi-square exceeds .01 level of confidence for one degree of freedom.
**Highly significant.

TABLE 12. Numbers of collections in three groups of total *Dermacentor variabilis* per collection classified according to nesting activity.

Nesting Activity		Total *Dermacentor variabilis* per Collection			Total Collections
		0	1	2 or more	
Observed Occupied	Expected	255	14*	6*	275
	Observed	226	32	17	
	Deviation	−29	18	11	
Unoccupied 1 - 4 Weeks	Expected	393	21*	9*	423
	Observed	366	39	18	
	Deviation	−27	18	9	
Abandoned	Expected	1046	56*	25*	1127
	Observed	1084	33	10	
	Deviation	38	−23	−15	
Never Observed Occupied	Expected	315	17*	7	339
	Observed	333	4	2	
	Deviation	18	−13	−5	
Total Collections		2009	108	47	2164

Chi-square: 107.27**
Degrees of freedom: 6
*Chi-square exceeds .01 level of confidence for one degree of freedom.
**Highly significant.

TABLE 13. Numbers of collections in three groups of total *Dermacentor variabilis* per collection clasified according to season.

Season		Total *Dermacentor variabilis* per collection			Total Collections
		0	1	2 or more	
Winter	Expected	397	21*	9	427
	Observed	424	3	0	
	Deviation	27	−18	−9	
Early Spring	Expected	367	20	9	396
	Observed	349	30	17	
	Deviation	−18	10	8	
Late Spring	Expected	368*	20*	9*	397
	Observed	315	53	29	
	Deviation	−53	33	20	
Summer	Expected	626	33*	15*	674
	Observed	661	12	1	
	Deviation	35	−21	−14	
Fall	Expected	251	14	5	270
	Observed	260	10	0	
	Deviation	9	−4	−5	
Total Collections		2009	108	47	2164

Chi-square: 181.61**
Degrees of freedom: 8
*Chi-square exceeds .01 level of confidence for one degree of freedom.
**Highly significant.

groups: 0, 1, 2 or more *D. variabilis* per collection. The first test of this set had as the second attribute the nesting activity of the mice (Table 12). The hypothesis that the total number of *D. variabilis* per collection was independent of the nesting activity of the mice was rejected because the total chi-square exceeded .01 level of confidence. The last test of this set had the season of the collection as the second attribute (Table 13). The hypothesis that the total *D. variabilis* per collection was independent of the season was rejected because the total chi-square exceeded the .01 level of confidence.

One assumption underlying the two tests of each set was that when the effect of one factor was studied, the other factor did not add any heterogeneity to the collection. One additional test to determine the effect of season upon nesting activity was performed (Table 14). The hypothesis of this test that the nesting activity of mice was not influenced by the seasons was rejected because the total chi-square exceeded the .01 level of confidence.

DISCUSSION

In this study the fluctuations in numbers and kinds of mites leaving nests are analyzed according to two complex factors of the environment: the seasonal climatic changes and the nesting activity of the mice. Any differences in the numbers and kinds of mites

TABLE 14. Numbers of collections in nesting activity groups classified according to season.

Season		Nesting Activity Groups				Total Collections
		Observed Occupied	Unoccupied 1-4 Weeks	Abandoned	Never Observed Occupied	
Winter	Expected	55	83*	222*	67*	
	Observed	51	56	185	135	427
	Deviation	−4	−27	−37	68	
Early Spring	Expected	51*	77	206*	62*	
	Observed	82	92	128	94	396
	Deviation	31	15	−78	32	
Late Spring	Expected	50	78*	207*	62*	
	Observed	57	156	153	31	397
	Deviation	7	78	−54	−31	
Summer	Expected	85*	132*	351*	106*	
	Observed	22	67	534	51	674
	Deviation	−63	−65	183	−55	
Fall	Expected	34*	53	141	42	
	Observed	63	52	127	28	270
	Deviation	29	−1	−14	−14	
Total Collections		275	423	1127	339	2164

Chi-square: 480.47**
Degrees of freedom: 12
*Chi-square exceeds .01 level of confidence for one degree of freedom
**Highly significant.

leaving the nests attributed to the factor of season are actually manifestations of the reactions of the mites to changes in the cliamatic conditions of the area. The activity of the mice includes their: (1) visiting the nest-funnels, (2) bringing in nesting material, (3) living in and abandoning nests, and (4) bringing in food. All these activities of the mice are part of the environment of the mites in the nest-funnels. The factor of the activity of the mice includes all of the four components of the environment mentioned by Andrewartha & Birch (1953). The mice live in the nest and their bodies generate heat; their urine adds moisture to the nests—component one, weather. Mice bring in food; they provide food for the mites such as hair and feces—component two, food. Mice serve as food for some mites, and eat other mites—component three, other animals. Mice bring in material when they build nests—component four, a place to live.

In order to determine the effect of any one of the two factors on the numbers and kinds of mites leaving the nests, the effects of the other factor must be such that changes in numbers and kinds of mites leaving the nests will be the result of reactions of the mites to changes in any one factor of the enviroment at a time. The observed fluctuations can be attributed to changes in one factor of the environment while the effect of the other is constant. For example, the number of collections from nest-funnels in which mice were observed in the winter or any season should not differ from the expected number of collections. If there are more or less than expected, then there will be unequal nesting activity in that season. If the inequalities continue from season to season, some with more nesting than expected and others with less, when the collections are grouped according to the seasons, any differences in numbers and kinds of mites escaping may be the result of seasonal differences or differences in nesting activity.

The collections from nest-funnels which were observed occupied, abandoned, etc., were unequally distributed among the five seasons so that the reaction of the mites to the seasonal climatic conditions also was influenced by the nesting activity of the mice (Table 14). There was more nesting than expected in early spring and less than expected in summer. The results of the analysis of fluctuations in numbers and kinds of mites escaping from nests cannot be attributed alone to the reaction of the mites to the factor of season, but also include reactions of the mites to nesting activity of the mice.

SPECIES OF ACARINA ENTERING NESTS

There were 141 species of Acarina collected from the nest-funnels. The species collected were used as a measure of the number of species which entered the nests above the funnels. No species could have been collected in a funnel unless it had passed through the straw or nest above the funnel. The number of species collected from funnels at various times during the history of the nest-funnels was used to determine the mode of entry of the species collected from the nest-funnels.

There must be some way for mites to enter the nest if the nest is in a tree, under the eaves of a house, etc. Norberg (1936) postulated that arthropods, including mites, could reach the nests by four means: transportation on nest material, transportation on the host animal, chance access, and deliberate entrance. The last method was studied experimentally and he found that some species do search for a nest actively but that Acarina were not among these species. Woodruffe (1953) listed five possible methods by which arthropods could colonize birds' nests: (1) attraction of flying adults, (2) attraction of crawling adults or larvae, (3) conveyance as food by insectivorous birds, (4) conveyance on nesting materials, and (5) conveyance on the birds. He also stated that methods 4 and 5 are adequate to explain the observed frequency of occurrence of mites in nests.

The board-funnels were constructed so that mice could not nest in or even visit them. There were only 4 species of mites collected from these board-funnels. These species represent 3% of the total number of species collected. Thus, 97% of the species were recovered from nest-funnels after mice had become a factor in the environment. The collections from the nest-funnels that were never observed occupied yielded 44 species of mites and 2 species of ticks. Because of the differences in the numbers and

feeding types of the species collected from the never observed occupied nest-funnels and the board-funnels, and the similarities of the relations of the number of species in the three dietary groups collected from the nest-funnels before they had been occupied and from nest-funnels when they were occupied, unoccoupied 1-4 weeks, and abandoned, the species of mites in collections from never observed occupied nest-funnels were considered to be a sample of not only the mites in the environment but also the mites carried by *P. leucopus*.

Mice could have entered the nest-funnels and stayed there for a short period of time. During this period, the mites which were on the mice could leave the mice and enter into the straw of the nest-funnels. These mites would be collected eventually in bottles beneath the funnels.

The length of time that a species of mite would stay in the nest would depend upon many environmental factors in the nest. The presence of a mite in the collection from any one period does not mean that the conditions in the nest when the mite entered were the same as when the collection was made. During the never observed occupied period, mites entered the nest-funnels either on the mice themselves, on some other animal which visited the nest-funnels, or from the general habitat. Of the 46 species of Acarina collected from the nest-funnels before they were observed occupied, 44 were not collected from the board-funnels. Only 7 of these 44 species were parasites of the mice, but several studies have reported (Morlan 1952; Ellis 1955) that small mammals carry many predaceous and miscellaneous feeding mites as well as parasites.

When mice built nests in the nest-funnels, they brought in nesting material of strips of bark, leaves, dried grass, feathers, hair, and other materials. When mice were observed in the nest-funnels, the collections from these funnels were placed in the observed occupied category; this was also the period when mice were building nests in the nest-funnels. There were 63 species of Acarina collected from the nest-funnels when they were observed occupied. In order to include the mites which were brought in on the nesting material but did not leave until after the period of occupancy, species collected from the nest-funnels which were unoccupied 1-4 weeks were included with the species collected from the observed occupied nest-funnels. There were 76 species collected from nest-funnels during the period 1-4 weeks after they were abandoned by the mice. Of the 92 different species collected from the nest-funnels which were occupied or unoccupied 1-4 weeks, 55 were not in collections from the board-funnels or from nest-funnels which had never been observed occupied. These 55 species, which were not collected from the environment or from the mice, were then considered to have been carried into the nest-funnels on the nesting material (Table 2).

Of the total species of Acarina collected from the board-funnels and nest-funnels, 73% can be allocated to three modes of entry: 3% of the species entered from the habitat without the aid of the mice; 31% were carried in on the mice themselves; 39% were carried in on the nesting material brought in by the mice. There were many means by which the rest of the species (27%) could have entered the nest-funnels. Species of mites could have been associated with inhabitants of the nest-funnels other than *P. leucopus*. Black snakes, a tree toad, ants, wasps, and bees also were found in the nest-funnels. Mites could have also entered on the nesting material or on the mice, but did not leave the nest area until some time after the nests had been abandoned. Some mites could have entered nest-funnels from the environment after a nest had been built in the nest-funnels as well as before any nest had been constructed in the nest-funnels. Of all the species collected from the nest-funnels, 70% were present because of association with the mice, either on the mice or in the nesting material that the mice brought into the nests. There were only 4 species in the habitat before the mice visited and nested there, but after the mice entered the habitat, there were 137 more species collected. Mice are directly involved in bringing Acarina into nests.

To see whether or not mice in nests attracted mites to the nest-funnels, nest-funnels were placed in the field which had mice imprisoned in them. The mice did not have free access to the general habitat and there were only three species of mites collected from these nest-funnels. The nests were established and the mice were living in them continuously, yet there were only three species collected from these nest-funnels. The three species that were collected from these occupied nest-funnels had also been collected from the other nest-funnels. These species were in the group which had been brought into the nests on mice (Table 2). These species may have been attracted to the nest-funnels by the mice in them; however, since these were carried by the mice, it seems more probable that the mites had been brought to the nests by mice which had visited the nest-funnels. Nicholson (1941) showed that the mice changed their place of residence often and they moved about in the study area. Mice may have visited these occupied nest-funnels and, although they could not enter them, they would have remained on the roof, by the opening, etc., long enough for these mites to leave the mice and enter the nest-funnels. Because these mice were not able to get outside the nest-funnels and bring in nesting material from the habitat, few species were collected from the nest-funnels. This again emphasized the role that mice play in bringing in Acarina on themselves or on nesting material.

SPECIES OF MITES LEAVING NESTS

The nesting activity of the mice affected the number of species per collection (Table 6). During the period when mice were in the nests or within 1-4 weeks after mice had left the nests, there were more species per collection than expected. Also before the mice constructed nests in the nest-funnels and after the nest-funnels had been abandoned for more than four weeks, there were fewer species per collection than

expected. When mice were living in nests in the nest-funnels, there were more species being brought into the nests than at any other time during the "history" of a nest-funnel. Before mice constructed nests in the nest-funnels there were few species collected, but some were carried in on the mice or entered actively. Species which were carried in on the mice or nesting material were still leaving the nests after the mice had deserted the nests, but not in the quantity which were leaving when mice were in the nests or 1-4 weeks after the mice had left the nests. While mice were in the nests there were more species leaving per collection than expected so that the mice not only bring in mites but also are a factor in determining whether or not mites remain, live, and reproduce in the nests.

The seasons influenced the distribution of the number of species per collection (Table 7). The number of species per collection was larger than expected in early spring and smaller than expected in summer. This was partially the result of unequal nesting in these two seasons. There was more nesting than expected in early spring and less nesting than expected in summer (Table 14). The collections from nest-funnels which were observed occupied by mice yielded more species per collection than expected. Because nesting was distributed unevenly throughout the seasons, differences in numbers of species per collection attributed to the effect of seasonal climatic conditions were also attributed to the effect of nesting activity of the mice.

The total chi-square of an R x C test was a measure of the amount of variation introduced into the distribution of the number of species per collection classifying the collections according to the divisions of any environmental factor such as nesting activity of the mice. The more variation or heterogeneity introduced into the distribution of the collections, the higher the chi-square. The values of the tests involving number of species per collection were: nesting activity (Table 6), 498.60 for 9 degrees of freedom; and season (Table 7), 192.68 for 12 degrees of freedom. Since both chi-square values are highly significant, both factors, nesting activity of the mice and seasonal climatic conditions, had an effect on the total species of mites collected from the nest-funnels. However, there was a relation between seasonal periods of more nesting than expected and seasonal periods of more species collected than expected. There was significantly more nesting in early spring and less in summer and there was also significantly more species per collection in early spring and less in summer. It was difficult to evaluate the effect of the seasonal climatic conditions because differences in the number of species per collection attributed to this factor could also be due to the effect of nesting activity.

There were not only fluctuations observed in the kinds of mites leaving the nest-funnels, but also fluctuations in the numbers of mites leaving the nest-funnels. The kinds of mites which escaped from the nest-funnels were used as a measure of the kinds that had entered the nests; the number that escaped was a measure of the productivity of the nests. A species of mite may be found in the nest-funnel, but whether or not that mite will survive and reproduce in the nest depends upon the nest's being a suitable place for the mite to live. The "suitability" of a nest for survival of a species depends upon two factors: the environmental requirements of the species and the environment provided in the nest. If the two agree, then the species will survive and reproduce; but if they do not agree, then the species will not find the nest a suitable area for survival and reproduction. At any one stage in the "history" of a nest-funnel, the conditions of the environment may be optimum for a few species and pessimum for others. For this reason the total number of mites that escaped per collection was not used as a measure of the optimum or pessimum of the conditions in the nest. The fluctuations of the number of *H. glasgowi* and *D. variabilis* which left the nest-funnel each week were used to determine the relative effect of nesting activity and seasonal climatic conditions upon these species.

By the technique used in this study, collections were not taken directly from the nest, but rather they consisted of those mites which left the nest area. Combined with the conditions which are favorable for the production of mites in the nest are other conditions which determine whether or not mites leave the nest. The number of mites collected each week from a nest-funnel depended upon the factors which influenced production of mites in the nest and determined whether or not the mites would remain in the nest. Conditions of the environment of the nest which determine whether or not a species could reproduce, survive, and leave the nest vary according to the requirements of each species.

NUMBERS OF MITES LEAVING NESTS

The total numbers of mites collected from each nest-funnel varied from nest-funnel to nest-funnel and also from collection to collection from a single nest-funnel. There was a relation between the distribution of the number of mites per collection and the activity of the mice in the nests (Table 8). There were fewer mites per collection than expected from the nest-funnels which were never observed occupied, more mites than expected per collection from the nest-funnels which were observed occupied and 1-4 weeks after occupation, and fewer mites than expected per collection from nest-funnels which were abandoned. During the observed occupied period, the mice were living in the nest, bringing in nesting material, creating food, and serving as food. It was a period when mice were exerting their greatest influence over the environment of the nest. This was a time of rapid change in the microenvironments of the nest; new mites were being introduced, reproduction of parasites occurred, and additional food sources were provided.

The unoccupied 1-4 weeks period was a time of change; the host animal had left, certain food sources were no longer available, and little new food or mois-

ture could be brought in. The conditions which were optimum for many mites when the nests were occupied must have become pessimum when the host had left, for more mites than expected left during the 1-4 weeks after the nest-funnels were occupied. Before the nest-funnels had nests built in them and were observed occupied, the number of mites per collection was less than expected. The conditions in the nest-funnels were "suitable" for some mites during this time and the relative stability of this period is reflected in the fact that few mites left the nests. After nests had been abandoned for 1-4 weeks, the effect of the mice diminished, and the changes in the nests which were associated with the presence of the mice were absent. Stable conditions, although different from the stable conditions before the mice entered the nest-funnels, were present in the nests by this period.

When the total mites per collection were classified according to seasons of the collections, there was some heterogeneity noted (Table 9). Seasons in which the greatest deviations were noted were early spring and summer. Early spring had more mites per collection than expected while summer had fewer mites per collection than expected. Early spring had more collections than expected from observed occupied nest-funnels and summer had fewer collections than expected from observed occupied nest-funnels (Table 14). Because more mites left the nests than expected during the period of nesting, unequal distribution during the seasons of collections from nest-funnels which were observed occupied would affect the distribution of the number of mites per collection when the collections were grouped according to the season. Although the seasonal climatic conditions as a factor of the evironment did affect the fluctuations in numbers of mites leaving nests, this influence could not be separated from the influence of the nesting activity.

The heterogeneity reflected in total chi-square in the distribution of the number of mites per collection caused by grouping the collections according to the two factors was as follows: nesting activity (Table 8), 492.67 for 12 degrees of freedom; season (Table 9), 157.56 for 16 degrees of freedom. Although many different kinds of mites had different environmental requirements, the collections from nest-funnels which were unoccupied for 1-4 weeks contained more mites per collection than collections from nest-funnels which were never observed occupied or abandoned.

NUMBERS OF *Haemolaelaps glasgowi* LEAVING NESTS

The numbers per collection of a single species of mite, *Haemolaelops glasgowi*, were also recorded. The fluctuations in the number per collection were studied to determine the effects of the environmental factors upon numbers of a single parasitic species escaping from nests.

The number of *H. glasgowi* per collection was affected by the nesting activity of the mice in the nest-funnels (Table 10). The number per collection from nest-funnels before mice had built nests or were observed in them was less than expected. There were more *H. glasgowi* per collection than expected from nest-funnels which were observed to be occupied by the mice or just recently abandoned, and less than expected per collection from nest-funnels in which nests had been abandoned for more than four weeks.

Since these mites are dependent upon the mice for their food, when a mouse is present in the nest, large populations of the mites would be built up in the nest. This would account for mites of this species which were collected from nest-funnels while mice were present in the nests. After the mice had left the nests, the mites produced when the host had been available would be searching for food and thus they would leave the nests and be collected from the nest-funnels. There were more mites per collection from nest-funnels not only when they were occupied, but also 1-4 weeks after the occupied period. Before the nest-funnels were occupied, *H. glasgowi* would be found in the collections only if they had entered on the mice themselves. There were few *H. glasgowi* collected from the nest-funnels which were never observed occupied. The collections from the abandoned nest-funnels contained some *H. glasgowi* which could have been produced when the nests were occupied and left nests later than four weeks after nests had been deserted by the mice.

The numbers of *H. glasgowi* per collection were also affected by seasonal climatic conditions (Table 11). Although these are both highly significant total chi-squares, the observed differences of more *H. glasgowi* per collection than expected in early spring and fewer than expected in summer can be explained not only by seasonal differences but also by differences in nesting of the mice in the nest-funnels during these two seasons. The amount of heterogeneity introduced into the distribution of *H. glasgowi* per collection shows the effect of the two factors of the environment. The total chi-squares are: nesting activity (Table 10), 216.43 for 9 degrees of freedom; season (Table 11), 170.45 for 12 degrees of freedom.

NUMBERS OF *Dermacentor variabilis* LEAVING NESTS

The number of *D. variabilis* was affected by the nesting activity of the mice (Table 12). There were more *D. variabilis* collected from the nest-funnels in which mice were observed and from nest-funnels which had been recently abandoned by the mice than from nest-funnels before mice had been observed in them or which had been abandoned for more than four weeks.

Numbers of *D. variabilis* per collection were also affected by seasonal climatic conditions (Table 13). There were more *D. variabilis* per collection in late spring than in any other season. There were also more *D. variabilis* than expected in early spring and less than expected in summer, fall, and winter.

The amount of heterogeneity introduced into the distribution of *D. variabilis* per collection shows the effect of the two environmental factors. The total chi-squares are: nesting activity (Table 12), 107.27 for 6 degrees of freedom; season (Table 13), 181.61 for 12 degrees of freedom. Both nesting activity and season had a marked effect on the numbers of *D. vari-*

abilis. The life history of *D. variabilis* as presented by Smith, Cole, & Gouck (1946) states that activity of immature stages reaches a peak from March through May and that during the rest of the year they are rare or absent. This tick does not breed in the nest; each specimen collected from a nest was carried into the nest. The activity of the ticks as influenced by seasonal climatic conditions is reflected in the number brought into and then captured from the nest-funnels. It the ticks are not active, they will not be collected even if mice are living in the nest-funnels. It is also true that ticks will not be collected in the nest-funnels unless their hosts carry them into the nests. Clearly then, both factors act to limit the numbers of *D. variabilis* that will be collected by this method.

The nesting activity of the mice was the major factor influencing the fluctuations of total species of mites per collection, total mites per collection, and numbers of *H. glasgowi* per collection. In contrast to this, the seasonal climatic conditions were a major feature influencing the fluctuations in numbers of *D. variabilis* per collection. There were more species of mites, *H. glasgowi*, and *D. variabilis* collected when the nest-funnels were either occupied or recently abandoned by the mice than before the nest-funnels were occupied or abandoned for more than four weeks. The peak of the number of species, number of mites, and number of *H. glasgowi* per collection was in early spring, as was the number of collections when mice were in the nests. The peak of *D. variabilis* was in the late spring, after the peak of nesting.

There is a basic difference between *H. glasgowi* and *D. variabilis* in their relation to the host and the nest. *D. variabilis* utilizes several different hosts throughout its life cycle, spends much time associated with its hosts, and does not breed in the nest so that collecting these ticks from the hosts, as is the procedure in surveys of ectoparasites, would give an accurate estimate of the total number of ticks in the environment. However, in the case of *H. glasgowi* breeding takes place in the nest and thus the nest as well as the host can harbor these mites in all periods of the year. In this case, ectoparasite surveys would collect those mites on the host but would not include mites escaping from the nests of the hosts.

SUMMARY AND CONCLUSIONS

An apparatus, the nest-funnel, that enabled continuous collection of Acarina escaping from nests of *Peromyscus leucopus noveboracensis* was developed. The nest-funnel consisted of a nest-box which had a hardware cloth floor to which a funnel was attached. A jar which contained liquid was attached to trap the mites and ticks. Jars were exchanged on 32 nest-funnels at weekly intervals for 96 weeks and the Acarina collected in this manner were counted and indentified. At the time the Acarina were collected, the nest-funnels were inspected for mice and the maximum and minimum temperature for the week were recorded. An R x C chi-square analysis was used to determine the effect of seasonal climatic conditions and nesting activity upon fluctuations in total species of mites, total number of mites, number of *Haemolaelaps glasgowi*, and *Dermacentor variabilis* per collection. There were 139 species of mites and 2 species of ticks collected from the nests. Of the Acarina, 18 species (12.8%) were parasites, 87 (61.7%) were predators, and 36 (25.5%) were miscellaneous feeders. Nesting activity of the mice was the major factor involved in bringing various species of mites into the nests. There were 4 species collected from funnels which had not been visited by mice. Forty-four additional species were carried into the nest-funnels on the mice, 55 additional species were carried in on the nesting material which the mice brought into the nest-funnels, and the rest, 38, could have entered by various means. There were 17,201 mites and 249 ticks collected from the nests. Of the mites, 4,983 (29.0%) were parasites, 3,638 (21.1%) were predators, 6,166 (35.9%) had miscellaneous feeding habits, and the feeding habits of 2,414 (14.0%) could not be determined. Included in the total parasitic mites were 1,748 *Haemolaelaps glasgowi*. The nesting activity of the mice was the environmental factor which had the most effect on fluctuations of species of mites, numbers of mites and numbers of *H. glasgowi* leaving nests. However, seasonal climatic conditions had an equal effect on the numbers of *D. variabilis* leaving the nests.

LITERATURE CITED

Allred, D. M. & D. E. Beck. 1953. Mite fauna of woodrat nests in Utah. Proc. Utah Acad. Sci. Arts & Letters. **30:** 53-56.

Andrewartha, H. G. &. L. C. Birch. 1954. The distribution and abundance of animals. Chicago: U. of Chicago Press. 782 pp.

Baker, E. W. & G. W. Wharton. 1952. An introduction to acarology. New York: The Macmillan Co. 465 pp.

Berlese, A. 1905. Apparecchio per raccogliere presto ed in gran numero piccolo artropodi. Redia **2**(1): 85-89.

Bishopp, F. C. 1923. The rat mite attacking man. U. S. Dept. Agric. Circ. **294:** 1-10.

Camin, J. E. & F. E. Gorirossi. 1955. A revision of the suborder Mesostigmata (Acarina), based on new interpretations of comparative morphological data. Chicago Acad. Sci. Special Pub. **11:** 1-70.

Cole, L. C. & J. A. Koepke. 1947. Problems of interpretation of the data of rodent ectoparasite surveys. Suppl. 202, U. S. Publ. Health Reports **62:** 1-24.

Cunliffe, F. 1955. A proposed classification of the trombidiforme mites (Acarina). Proc. Ent. Soc. Wash. **57** (5): 209-218.

Drummond, R. O. 1955. An apparatus for the continuous collection of ectoparasites from nests of small mammals. Jour. Parasitol. **41** (6-sect. 2): 37-38.

Ellis, L. L., Jr. 1955. Study of ectoparasites of certain mammals in Oklahoma. Ecology **36**(1): 12-18.

Garman, P. A. 1937. Bird mites in a dwelling house. Bull. Connecticut Agric. Expt. Sta. **396:** 406-407.

Hughes, A. M. 1948. The mites associated with stored food products. London: Minist. Agric. Fish. H.M.S.O.: 1-168.

Jackson, W. B. 1953. Use of nest boxes in wood mouse population studies. Jour. Mammal. **34**(4): 505-507.

Linsdale, J. M. & L. P. Tevis, Jr. 1951. The dusky-footed wood rat. Berkeley and Los Angeles: Univ. Calif. Press, 664 pp.

Linsley, E. G. 1944. Natural sources, habitats, and reservoirs of insects associated with stored food products. Hilgardia **16:** 187-224.

Morlan, H. B. 1952. Host relationships and seasonal abundance of some southwest Georgia ectoparasites. Amer. Midland Nat. **48**(1): 74-93.

Nicholson, A. J. 1941. Homes and social habits of the wood-mouse, *Peromyscus leucopus noveboracensis* in Southern Michigan. Amer. Midland Nat. **25**(1): 196-233.

Norberg, S. 1936. Biologish-ökologische untersuchungen uber die vogelnidicolen. Acta Zool. Fennica **21:** 1-168.

Oudemans, A. C. 1913. Acarologisches aus maulwurf-nestern. Tijdschr. Ent. **57:** 62-78.

Ross, E. S. 1944. Arthropod collecting in burrows of a Texas pocket-gopher. Ent. News **45**(3): 57-61.

Sambon, L. W. 1928. The parasitic acarians of animals and the part they play in the causation of the eruptive fevers and other diseases of man. Preliminary considerations based on an ecological study of typhus fever. Ann. Trop. Med. and Parasitol. **22**(1): 67-132.

Smith, C. N., M. M. Cole, & H. K. Gouck. 1946. Biology and control of the American dog tick. U. S. Dept. Agric. Tech. Bull. **905:** 1-74.

Snedecor, G. W. 1946. Statistical methods. Ames: Iowa State College Press. 485 pp.

Tullgren, A. 1917. En enkel apparat för automatiskt vittjande av sållgods. Ent. Tidski. **38:** 97-100.

Vysotska, S. O. 1947. Seasonal dynamics of the parasitic fauna of *Microtus arvalis* and the inhabitants of its nests in the vicinity of Leningrad (in Russian). Zool. Inst. Ak. Nauk. SSSR: 1-143.

Walters, R. D. & V. D. Roth. 1950. Faunal nest study of the woodrat *Neotoma fuscipes monochroura* Rhoads. Jour. Mammal. **31**(3): 290-292.

Wharton, G. W. 1946. Observations on *Ascoschöngastia indica* (Hirst, 1915). Ecol. Monogr. **16**(3): 151-184.

Woodruffe, G. E. 1953. An ecological study of the insects and mites in the nests of certain birds in Britain. Bull. Ent. Res. **44:** 739-772.

Woodruffe, G. E. & B. V. Southgate. 1951. Birds' nests as a source of domestic pests. Proc. Zool. Soc. London **121**(1): 55-62.

Yunker, C. E. 1955. A proposed classification of the Acaridiae (Acarina: Sarcoptiformes). Helminthol. Soc. Wash. Proc. **22**(2): 98-105.

THE VICUÑA AND THE PUNA

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INTRODUCTION

High in the central Andes of western South America, above the limit of cultivated crops, lies a treeless pastoral zone, the puna. While scanning the bleak rolling grasslands of the puna a traveler may be startled by a prolonged screech. The cry attracts his gaze to a racing troop of fifty gazelle-like mammals, bright cinnamon in color—vicuñas! As they gallop up a barren slope he sees that a single large vicuña pursues them closely. The pursuer charges at one straggler, then another, as if to nip its heels. But suddenly the aggressor halts, stands tall with slender neck and stout tail erect, stares at a line of llamas in the distance, and whistles a high trill. Then it gallops away to join a band of several vicuñas, some obviously young, which graze close by. And these it follows as they file uphill, away from the approaching llamas and the somber Indian who trudges behind them.

The barefoot herdsman tells the traveler that the small retreating band is a family of vicuñas, females and young, protected from the rear by their leader, an adult male, and that the large fleeing troop consists entirely of males. The traveler sees no difference in the appearance of the supposed sexes. On reflection, however, he recalls that the vicuña is reputed to spend its life at heights reached only by the most lofty peaks in his own country, and that it bears a costly fleece which, centuries ago, clothed Inca royalty. To him the vicuña resembles, in size, actions, and habitat, the pronghorn antelope of the Great Plains. But inasmuch as the vicuña has a long neck and rather large feet, and lacks horns, it is more like a small humpless camel.

The vicuña and other llama-like ungulates, or lamoids, are of the camel family (Camelidae). The fossil record indicates that this family originated and developed in western North America, spread via land bridges into Asia and South America, and finally became extinct in its original homeland. In the Old World two species of camelids survive: the Bactrian camel and the Dromedary. These two (genus *Camelus)* are much larger in size than any of the four species that live in South America: the llama *(Lama glama)*, alpaca *(L. pacos)*, guanaco *(L. guanicoe)*, and vicuña *(Vicugna vicugna)*. Paleontological studies made in Argentina show that these species were distinct in the Pleistocene period. Yet, some authors consider that the llama was derived from the

FIG. 1. Trains of llamas carrying sacks of produce are a common sight in the puna. The tola shrubs and fescue grass are poor forage. Near Mazocruz, Puno; August 22, 1952.

guanaco, or that the alpaca is a hybrid between the llama and the vicuña, and others have expressed still different views (López Aranguren 1930; Gilmore 1950).

The four lamoids resemble one another in structure, but they differ in size, range, pelage, temperament, and usefulness to man. The llama is in common use by highland natives, from northern Peru to northern Chile and Argentina, for carrying burdens (Fig. 1). Trains of llamas march long distances over the inhospitable Andean highlands, descend westward to the arid coast, and eastward to the low humid jungles. Each llama may carry across its back a sack of dried potatoes or similar modest load. As do other domestic animals, llamas vary much in size, but the usual weight is about 200 pounds, considerably more than an alpaca and twice as much as a vicuña. Variable too is the color of llamas—black, white, and browns, in pure form, patchwork, or blends. Alpacas are usually of a solid color, as befits their primary use as producers of abundant long wool. Because they are capricious as compared to the stolid llamas, alpacas rarely carry burdens or walk great distances from their home pastures. They thrive only in Peru and Bolivia, and only at elevations above the level of Lake Titicaca, 12500 ft.

In contrast to the llama and alpaca, which have been domesticated for hundreds of years, the vicuña and guanaco are wild animals. Guanacos look much like llamas, but the color of their pelage is a fairly uniform reddish-brown. Although guanacos range from the highest grasslands to sea level, they are rather scarce in the range of the other lamoids, and they are most abundant near the southern tip of South America. Adults are of little commercial value, but the hides of the very young are prized by the natives for the manufacture of robes.

The phylogenetic classification of the lamoids seems to be indeterminate, at least on the basis of structural criteria. Of the group, the llama and guanaco are the most similar, and the vicuña, although resembling the alpaca in some characteristics, is the most distinct. It has been variously classified as specifically, subgenerically, or generically separate from the other lamoids. The characteristic, unique among living artiodactyls, that best supports generic separation of the vicuña is its peculiar lower incisors. In *Vicugna* these are very long with parallel sides, enamel on but one face, and an open root (Miller 1924:2). In contrast to these rodent-like incisors, those of *Lama* are short and wedge-shaped, with enamel on both faces and a closed root.

Another characteristic that distinguishes the vicuña from the other lamoids is the bib of long hair which

FIG. 2. At the approach of an intruder, an adult male vicuña postures with head and tail high, making himself appear as large as possible. Huaylarco, Department of Arequipa; March 11, 1952.

hangs from its brisket. This hair is white, like the rest of the under parts, and contrasts strongly with the dark buffy-brown hue of the upper parts (Fig. 2). Often differences in the tone of the dorsal color enable an observer to recognize individual vicuñas in a group. Some color differences are due to age. But apparently the sexes are alike in color.

As their wool is the finest known, and as their hides and meat are prized by the natives of the Andean highlands, vicuñas have been hunted for centuries. In many parts of its range the species is threatened with extinction. Man, therefore, has a moral obligation to take action to conserve the species, and an economic interest in perpetuating the supply of vicuña wool. Further, the vicuña is of great scenic value as the most conspicuous wild animal of the dreary puna, and it is unexcelled in lithe beauty.

Until now, no methodical study of the life of the vicuña has been made. Nearly all published summaries concerning vicuña habits are based on repetitions of the statements, many true but some false, of J. J. von Tschudi, a naturalist who traveled in Peru more than a century ago and who published a large volume on the Peruvian fauna (1844-1846, in German). The essential facts heretofore known about vicuñas and the other lamoids are well summarized by Cabrera & Yepes (1940:256-269) and by Gilmore (1950:429-454). The agricultural knowledge of lamoids have been reviewed by Cardozo (1954), Romero (1927), and Maccagno (1932). The only significant account of recent observations of wild vicuñas is that of Pearson (1951:161-168).

The present study is primarily a survey of the behavior of the vicuña in its native habitat, with emphasis on social relationships. Ecology, distribution, history, utilization, and management have been investigated in moderate degree in order to fill out a broad picture of the animal, its environment, and its relations with man.

The basic reason for this kind of study is that a sound program for the conservation and management of any wild animal must be based on scientific knowledge of the habits and environment of the species. This paper is a contribution to that knowledge. But further, detailed accounts of the actions of wild animals are fundamental to studies of comparative behavior, especially parallel and convergent evolution in behavior. And, as studies of morphology have not clearly determined the phyletic relationships among the lamoids, studies of behavior may clarify our understanding of these relationships.

The vicuña is an ideal subject for study by observation in its native surroundings. Groups of vicuñas may be watched for hours with relative ease, for they dwell on open grasslands, and they are large, gregarious, active by day, and not overly wary. Important to the investigator was the fact that the Andean highlands are healthful in climate and accessible by automobile, yet rather sparsely populated by man.

I am deeply grateful to an anonymous donor to the University of California, who provided funds for these studies. In the field I was accompanied and aided by Mary Koford. Assistance in making arrangements for the field work and hospitality were generously provided by Jávier Ortíz de la Puente, Sr. and Sra. Francisco Paredes, Dr. and Mrs. David P. Duffie, Dr. Guillermo Mann, William Rudolph, Paul Crum, Erik Neilsen, and Miguel Urdangarín. Identification of grasses was undertaken by Dr. John Reeder, Yale University; that of other plants by Dr. Helen Sharsmith, University of California. Drs. A. H. Miller and O. P. Pearson, Museum of Vertebrate Zoology, read the manuscript and made numerous helpful suggestions in the course of the work.

METHODS

Early in April, 1951, I first saw vicuñas in the wild. On this occasion, several groups were observed in southern Peru near the highest point of the road that runs eastward from the city of Arequipa to the town of Puno, which lies at the edge of Lake Titicaca in the department of Puno. After several weeks of search for a suitable study area in Puno, we established camp just east of the highest pass on the road from Tirapata to Limbani, at the extreme head of the Amazon (Inambari River) drainage, about 65 mi north of Lake Titicaca. This place, Aricoma, is situated at an elevation of about 15500 ft in an area of damp grasslands and clear lakes, close to glacier-flanked peaks. There we remained for a period of 5 months (May 24 to October 16). In May, and again in August, we spent several days at a vicuña ranch, Calacala.

About the middle of the year Indians and livestock began to interfere with studies at Aricoma, and these annoyances increased. Therefore, we sought a less

disturbed area in which to study birth, mating, and intergroup relationships. The site chosen was Huaylarco, which is located near the Arequipa-Puno road at a point about 55 mi west of Puno, at an elevation of 15000 ft, in an arid region of rolling hills and pampas. There we camped for a period of 6 months (November 7, 1951, to May 3, 1952).

On occasions we explored various other roads in southern Peru and briefly observed vicuñas in the vicinity. The principal sites of these observations were: the road over the cordillera between Chalhuanca and Púquio, about 200 mi northwest of Arequipa; between Macusani and La Raya, 120 mi north northwest of Puno; along the Crucero to Poto road, about 50 mi north of Lake Titicaca; near the road from Ocoruro to Imata, the latter 65 mi west of Puno; in the vicinity of Laguna Salinas, 25 mi east of Arequipa; near Lake Loriscota, 60 mi south of Puno; and, finally, adjacent to the road between Mazocruz and Tarata. This last road we traveled while driving from southern Peru to northern Chile.

In August, 1952, we entered the northernmost province of Chile, Tarapacá. The following month we camped for a week near Caritaya, 80 mi north northeast of Iquique. But we found vicuñas scarce there, so we drove on southward to the province of Antofagasta. There we stayed 5 weeks (October 2 to November 6, 1952) in the volcanic region about 55 mi northeast of Calama, and we saw vicuñas nearly every day. The span of time spent in the vicuña zone of the Andes was 18 months (April 1951 to November 1952), but as much time was spent in other tasks, only about 10 months were spent in field studies of the vicuña.

The principal method of study was to watch undisturbed groups of vicuñas from distant points with binoculars and a 20x telescope. Watching from long range, rather than from a close blind, is advantageous in that the observer can reach or leave his post without disturbing the animals, minor movements of hands or notebook pass unnoticed, and events occurring within a large area can easily be seen. Stone walls and native huts were often used as blinds, but where roads or terrain permitted I drove my car, a jeep with closed metal top, to the observation post. The car made a spacious and comfortable blind with cameras, maps, and other bulky equipment at hand.

An intimate acquaintance with the normal composition and behavior of many groups of vicuñas was necessary to the interpretation of actions observed. For understanding behavior the most valuable data, but the most tedious to obtain, were observations of a few well-known groups for long periods on successive days. In adjacent bands on successive days many factors of the environment that vary with place or time of year, such as weather, vegetation, and water, are relatively constant. Thus, the factors that cause variations in behavior can be recognized.

In the puna evening the cold is penetrating and writing or other work with the hands painful, except within a heated shelter. We found that a small trailer of standard design, modified to use kerosene for heat and a storage battery for light, made a comfortable home. The trailer remained at one site for many weeks at a time, while the jeep alone was used for short, rapid, or difficult trips.

DISTRIBUTION, POPULATION, AND MORTALITY

OCCURRENCE

To try to outline the entire range of the vicuña is presumptuous. Naturalists have reached few parts of the zone where vicuñas dwell. Specimens are few, specific records are scanty, and allusions by natives and tourists are indefinite. I have attempted only to sketch the approximate limits of the geographic range of the vicuña (Fig. 3). For the most part, the range outlined follows the elevation contour, judging the limit of the vicuña zone by the level of the nearest known occurrence. Many of these levels were determined by observations made from some of the dozen good dirt roads that cross segments of

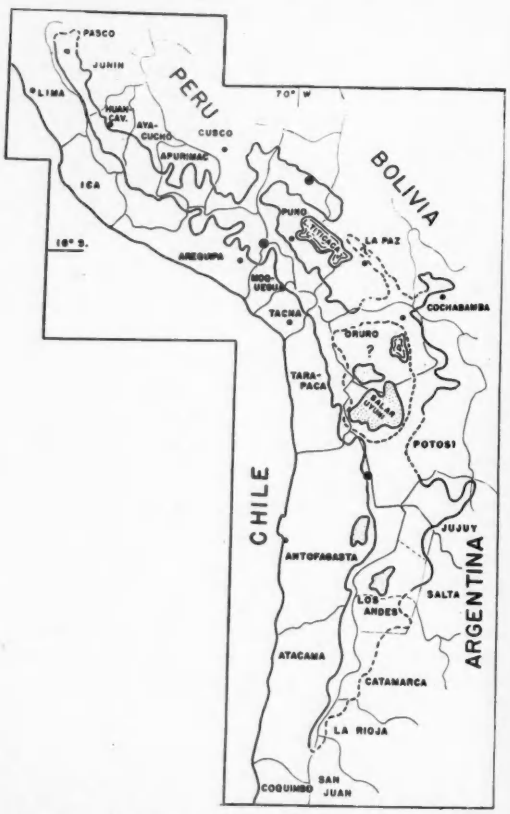

FIG. 3. Outline map of the present range of the vicuña. The limits of distribution are shown by the heavy solid line, broken portions indicating where the limits are most doubtful. The three large black dots indicate the principal areas of study, from north to south: Aricoma, Huaylarco, and northeastern Antofagasta. Smaller dots show locations of cities bearing the same names as the departments or provinces in which they are located.

the vicuña range. The accurate determination of the range of the vicuña and of the population densities in different regions would be a difficult but valuable project for future investigators.

The limits of the present and former range of the vicuña are discussed in the appendix. In general, the vicuña now occurs over an area 1300 mi in length, between the latitudes of 10° and 29° South. Although Allen (1942:410) considered the vicuña to be a vanishing species, perhaps already extinct in Chile, my review of the records suggests that the overall range may not have diminished within historical times. Doubtless there has been a decline in vicuñas in local areas heavily used by man. But in the last century or more, it appears that the activities of man and domestic animals have not greatly modified the general distribution of vicuñas. Insofar as stability of overall range of occurrence is a valid criterion of welfare, the vicuña does not seem to be approaching early extinction.

In elevation, vicuñas normally range as high as 16000 ft. Although they occur as low as 12000 ft, I estimate that at least two-thirds of the population lives above the 14000-ft level. In southern Peru I found vicuñas to be common only at sites above 14500 ft, and most abundant at about 15000 ft. The limits of range are apparently determined by availability of food and by freedom from disturbance, not by the rarity of the atmosphere.

HABITAT

Climate.—In the Southern Hemisphere summer commences in December, autumn in March, winter in June, and spring in September. In the puna summer is the wet season, as in the grasslands of central North America. At many puna localities more than ¾ of the annual rainfall of about 25 inches falls in summer. But because, even in summer, the air is cold at high elevations, summer in the puna is a time of snow and hail, and it is locally known as "invierno" (winter). At the end of summer plants are green and water is widespread. Then during autumn, vegetation and soil become dry, and drier yet in winter when skies are often cloudless.

In the United States spring is typically a season of awakening from dormancy for both plants and animals. Plants grow rapidly as the sun warms moist soils. Most animals produce their young. But in the puna spring brings warmth to ground already dry. Green food is scarce; few animals bear young. Then, with the coming of summer rains and snows, moisture and warmth favor abundant plant growth. Vicuñas and most other puna mammals are born in summer, although for humans the weather is then miserable. The climate of the Peruvian puna has been described by Bowman (1916), Weberbauer (1945), and Pearson (1951). Probably similar is the puna climate of Bolivia, Argentina, and Chile, although south of Lake Titicaca the highlands are generally more arid than in Peru.

The climate of the mountains northeast of Lake Titicaca, where studies were made at Aricoma on the eastern slope of the Cordillera de Carabaya, is less typical of the vicuña zone. This region is comparatively humid, for the trade winds which sweep westward over the damp Amazon jungles are lifted by the eastern slopes of the Andes and here drop their moisture. On the windward slopes of high peaks spectacular glaciers descend to a level of about 16000 ft. In 1951 at Aricoma, in the "dry" season the sky was cloudy nearly every day, evening fog was common, and snow fell in every month save July. But in spite of this dampness the grass, viewed from a distance, appeared brown and lifeless in winter and spring.

Temperature.—One might expect that even in the tropics the nights would be very cold at an elevation of nearly 3 mi. At Aricoma in winter and at Huaylarco in summer, I kept fairly complete records of daily maximum and minimum temperatures. With few exceptions, at neither locality did the nightly minimum fall below 18° F and on many occasions the minimum was above freezing. Winter minima were higher in humid areas, such as Aricoma, than in dry areas, such as Huaylarco. At Aricoma it did not freeze on some nights of the coldest months of the year, while at Huaylarco I recorded temperatures as low as 5° F in November, a few months after the coldest time of year. For a station west of Lake Titicaca at an elevation of 15500 ft, Bowman (1916: 161) gives the absolute minimum for one year as 0.2° F (June). Evidently, then, below zero temperatures are rare in the puna.

For the same high station Bowman gives the maximum temperature for one year as 70.4° F (December). The highest that I recorded in the puna of Peru was 61° F (Aricoma, September). It seems, then, that in the vicuña zone the highest and lowest temperatures are much less extreme than in many cities of central North America. The yearly temperature range of about 70° F in the puna is about a third less than the yearly range at Chicago.

Neither is the daily temperature range in the puna extreme. The greatest daily range that I noted was 50°F (Huaylarco, November). For one month (January) the maximum daily range at Huaylarco was only half as great. Daily ranges are generally higher in spring than in summer, for in the latter season the sky is frequently overcast. Daily maxima in summer may be no higher than in winter.

As compared with many grazing mammals of North America, vicuñas need withstand neither extreme cold, extreme heat, nor extreme variations in air temperature. But of great effect at high altitude is solar radiation. In thin air bodies absorb heat rapidly from the sun, and they lose it quickly when the rays of the sun are blocked. Moreover, wind, dry air, and low atmospheric pressure are all factors that increase the rate of evaporation. Puna organisms, therefore, must be able to cope with rapid changes in solar heat and with rapid rates of drying. Doubtless the dense fleece of the vicuña is of great importance in protecting the animal from weather extremes.

Water distribution.—At Huaylarco streams were dry by late October, the middle of spring. Rains commenced about Christmas. Several days later streams flowed fast and lake levels were rising. One lake spread and covered many acres of a pampa where vicuñas had grazed a few days earlier. In December numbers of Indians mined the thick white layer of salt in the bed of Laguna Salinas, east of Arequipa. But in January this bed of salt was replaced by a wide shallow lake, colored pink by several thousand Chilean flamingos. After the middle of February storms were few at Huaylarco, and by the end of April many streams were dry. Even at Aricoma, a far wetter area, many streams, seeps, and ponds dried up during the winter and spring.

Vegetation and food.—In most of the region inhabited by vicuñas the dominant plants are perennial bunch grasses. The larger tufts are about 1 ft in diameter but, because of heavy grazing, they are usually less than a foot in height. On the better grazing sites at Huaylarco the crowns of plants covered no more than 50% of the ground surface. Groups of low evergreen shrubs, or "tola," alternate with grasslands in various proportions, from isolated bushes to continuous stands. The principal species of tola are *Lepidophyllum rigidum, L. quadrangulare,* and *Baccharis microphylla* (all family Compositae). On occasions I saw dozens of vicuñas and hundreds of alpacas grazing on pampas where tola was dominant, though seldom browsed. In the areas of study, the lower altitudinal level of occurrence of vicuñas was often noted to be near the lower limit of *L. rigidum.* In the higher vicuña country mat-forming plants, cushion-plants, and rosette-plants, well-adapted to resist desiccation, are common. Many aspects of the phytogeography of the puna are discussed by Weberbauer (1945).

The principal food of vicuñas is grass. At Huaylarco, away from streams, the grasses most sought by vicuñas are *Calamagrostis brevifolia* and *C. vicunarum.* These are normally kept cropped to a height of 1-2 inches by grazing animals. They thrive well in the protection of tall coarse grasses, thorn bushes, and rocks, and near the edges of plant mats and dung piles. Commonly vicuñas feed on the grasses that border streams or grow on islets. Here the main forage grass is *Festuca rigescens,* which grows in compact blue-green tufts (Fig. 4). Pearson (1951:167) reported that this fescue was an important food of vicuñas at Caccachara, 60 miles southeast of Huaylarco. He also noted that *C. nitidula* was favored. Several other species of the genera *Calamagrostis, Festuca, Poa* and *Stipa* were grazed, in varying degree, by vicuñas at Huaylarco.

In many areas where vicuñas forage the most conspicuous plants are tufts of coarse bunch grasses.

FIG. 4. While a vicuña family stands in a cold running stream, one female feeds at a clump of bunch grass *(Festuca rigescens),* another urinates in the water, and a third spits at a yearling. The three females at the right appear to be pregnant. Huaylarco, Arequipa; February 25, 1952.

These are principally the sharp-tipped *Festuca orthophylla* and *F. dolicophylla*. Although these grasses are rarely nibbled by vicuñas, their roots are important in retarding wind and water erosion. And when snow blankets the ground, the stiff tufts break up the snow surface and expose adjacent herbage to grazing animals (Fig. 5). Further, the tall tough grasses protect short succulent plants from sun, wind, and the hoofs of livestock. So heavy is the grazing of livestock in some portions of the Peruvian highlands, however, that even the coarse grasses are often mowed to a stubble a few inches in height (Figs. 6 and 7).

Succulent forbs, mostly annuals that rise not more than half an inch above the ground surface, are relished by vicuñas. At Huaylarco a small legume, probably *Astragalus peruvianus*, was common and apparently sought by vicuñas. They pawed this plant from the soft ground and ate the upper roots, about a quarter inch in diameter, as well as the tiny leaflets and blue flowers. Near the end of the rainy season, short forbs grow in abundance between tufts of grass.

Viewed from a distance, many sandy pampas where vicuñas feed appear to have no vegetation (Fig. 8). Upon closer inspection, however, one finds that the ground is sprinkled with rosette plants, few larger than a pocket watch. In the early months of the year the even distribution of these plants is obvious, for each rosette bears a white flower. Apparently because of this white speckling, one plain where vicuñas dwell is named the Pampa de Confital (Candy Plain). Most of the rosettes that vicuñas eat are species of *Nototriche* (family Malvaceae). On average grazing sites these plants grow in a density of about five per square yard. On poor grazing sites plants cover as little as one thousandth of the ground surface. The most conspicuous plant that dots many barren hills is a large rosette with hairy aromatic leaves, *Werneria* (family Compositae), but this does not appear to be eaten by vicuñas.

At many moist sites in puna grasslands there are spongy bright green carpets, some more than 100 feet in width, of *Distichia muscoides* (family Juncaceae). Vicuñas may crop the shoots of these soaking wet mats. At drier sites pale-green carpets of *Pycnophyllum* (family Caryophyllaceae), rarely more than 5 ft across, cover patches of rocky soil and lend a green aspect to otherwise naked ground. Although vicuñas seem not to crop these dry mats, they commonly eat blades of succulent grasses that grow up through them.

Vicuñas and other lamoids deposit their dung in discrete piles. Most of the plants that grow on or close to these piles are conspicuously different from the plants of the surrounding pasture (Fig. 9). Early in the wet

FIG. 5. When snow covers the ground vicuñas feed on uncovered vegetation or thrust their muzzles down through the soft snow. These three are troop males. Huaylarco, Arequipa; March 4, 1952.

FIG. 6. Most of the members of male troops are immatures of about the same size. These six are probably yearlings. Livestock has grazed the coarse fescue in the foreground to a low stubble. Huaylarco, Arequipa; January 11, 1952.

FIG. 7. In feeding on short herbage, a vicuña ambles forward slowly, muzzle close to the ground. This pregnant female, damp from recent bathing, feeds between thorn bushes hedged by passing livestock. Huaylarco, Arequipa; February 27, 1952.

season grass shoots grow up through the edges of dung piles, and vicuñas crop these shoots. But the majority of plants that grow on dung are low annual forbs. Late in the wet season brilliant green circular spots mark the location of dung heaps, and on many barren hills these spots are the only greenery that can be seen from a distance. Near the crests of dung piles at Huaylarco, a nettle about an inch high, probably *Urtica flabellata* (family Urticaceae), grew thickly. Apparently vicuñas did not eat this, although they seemed to nibble the green carpet of another forb, *Arenaria* (family Caryophyllaceae), that grew about two inches high around the edges of the mounds. In general, the forbs on dung piles are not relished by vicuñas. What, then, is the advantage of concentrating the dung and urine? One possibly advantageous effect is that the excretory chemicals influence the vegetation on but a small fraction of the pasture.

Food and distribution.—The upper altitudinal limit of the vicuna rañge is apparently set by the lack of herbage at higher levels. Few plants grow in the cold desert above 16000 ft elevation. Surrounding Lake Titicaca, below the normal range of the vicuña, and bordering the puna on the eastern slopes of the Andes, is a belt of rainy-green shrubs and grass steppes. The grass in this zone is much taller than the bunch grass of the puna, and there is little bare ground between tufts. Even though human culture

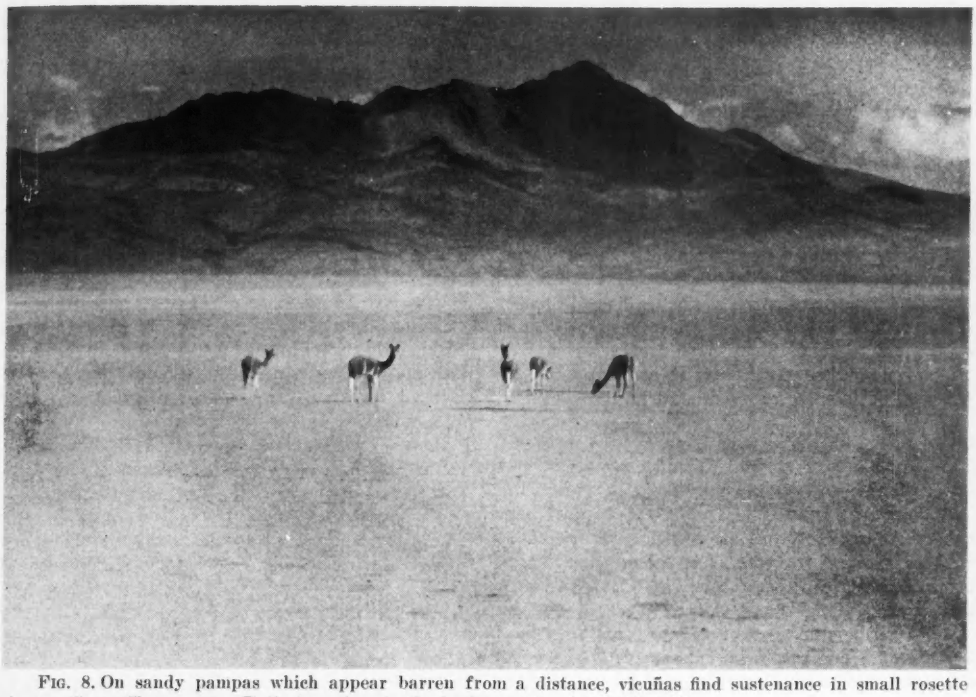

FIG. 8. On sandy pampas which appear barren from a distance, vicuñas find sustenance in small rosette plants. Cerro Chucca, near Pati, Arequipa, in the background. April 16, 1952.

FIG. 9. Although grass covers most of the surrounding ground, old dung piles are carpeted with short green forbs in summer. Here an adult male voids. The rocks are a temporary fireplace made by an Indian atop his fuel supply. Huaylarco, Arequipa; February 27, 1952.

did not prevent vicuñas from frequenting these lower grasslands, they might be unsuitable for grazing, for vicuñas feed mainly on short perennial herbs. Moreover, tall, thick grass would interfere with running. Nevertheless, a herd of domestic vicuñas seems to thrive near Lake Titicaca in the grass steppe zone at an elevation of 13000 ft.

In arid parts of the vicuña range it is probably also the lack of suitable food, principally green herbage, that determines the lower limit of occurrence of vicuñas. In Peru most of the western slopes of the Andes are barren. In northern Chile there is little grass cover, away from streams, below the 12000 ft level. Compared to the dry western slopes at somewhat lower elevations the puna is moist, and some green food is available there at all seasons. It is this greenery of the higher pastures that attracts shepherds and their flocks from lower elevations during the dry winter.

That green herbs are the preferred food of vicuñas was apparent from observations of feeding, and confirmed by the examination of the stomach contents of three animals. Furthermore, in dry regions vicuñas are most abundant where the soil is moist and the vegetation succulent. Where vicunas feed on small hairy plants, such as *Nototriche*, usually only the newest leaves are eaten. Roots that vicunas eat are carrot-like in texture, not woody. But on the other hand, very dry food is sometimes taken. Many times I saw a vicuña chew down a single dry stalk of coarse fescue. One, while crossing the dusty bed of a dried up pond, picked up a wad of desiccated algae in its mouth and chewed this several times before dropping it.

In order of decreasing requirement for succulence in food, I would rank the lamoids: alpaca, vicuña, llama, and guanaco. The fact that this is also the order of increasing geographic range suggests that the seasonal availability of green food and the differing ranges of tolerance of the lamoids for dry food

are important factors determining the limits of their distribution.

Soil.—The geology of the puna is complex. Evidently puna soils are fertile, but coolness and aridity limit plant growth. Damp sites are verdant. In the study areas the soil is pale in color, sandy in texture. Even in grasslands the soil is generally so loose that the footprints of birds and mice can be followed. Gravel is commonly mixed with the sand, and on barren pampas wind keeps the scattered gravel exposed as a moderate erosion pavement. Rocky slopes, cliffs, and rockslides are common. In walking and running on slopes and rocks, the lamoids are probably more adept than the Old World camels. The fact that the feet of lamoids are more deeply cloven than the feet of the other camels may be an adaptation for locomotion on hard or rocky ground.

POPULATION COMPOSITION

Specific meaning of terms.—Vicuñas are gregarious. They gather into two basic kinds of groups, here distinguished as *bands* and *troops*. A typical band is comprised of one adult male with several females and their young of the year. These *band females* and young together constitute the *family* of the male (the *family male* or *band male*). Year around the family of vicuñas occupies a certain piece of ground, the *territory*. The territorial boundaries are defended by the *resident male* (a family male on his own territory) against encroachment by alien males and *displaced bands* (family bands that are not on their own territories). Areas that are not defended are called *unclaimed* ground. It is well to note that the vicuña family is not a "harem," in the sense that the term has been used in studies of fur seals and red deer. In those species the harem exists only in the breeding season, and the females have no attachment to the male or his territory, except through having been captured by him and prevented by him from leaving (Dice 1952: 242-244). Males that are not members of bands gather into leaderless *troops* consisting of many individual *troop males*. Most of these males are yearlings and two-year olds. In the sense that they have not yet mated, most troop males are "bachelors," but as this term has special connotation for a certain age group of fur seals, I have avoided it.

In the study area, most vicuñas were born in March. The *young juveniles* become *old juveniles* at about six months of age (October 1, for convenience) and *yearlings* on January 1. Yearlings and two-year olds are recognized as *immatures* as contrasted to juveniles and adults.

Sex ratio.—In a polygynous society one might expect to find that females outnumber males in the total population. Because of the difficulty of quickly distinguishing the sex of a vicuña, the simplest method of determining the relative numbers of males and females is to compare the total number in bands (excluding juveniles, which may be of either sex) with the number in troops. For a 1:1 sex ratio and an average band size of 5 members, 42% of the non-juvenile vicuñas in a region would be troop males. This percentage would be lower for smaller bands, higher for larger. Does approximately such a proportion exist?

While traveling by auto through the open vicuña country, one can count the numbers of vicuñas seen in groups and attempt to classify the groups. With fair assurance, groups containing juveniles are family bands, and groups that have 15 or more members, but no juveniles, are male troops. Unfortunately, it is difficult to determine whether smaller groups that have no juveniles are bands or troops. If all these groups are assumed to be bands, the results of the census will give a very low percentage for males. Making this assumption, in one count of 315 vicuñas the indicated proportion of males was only 19%. Doubtless many of the small groups that were counted as bands were in fact troops.

Another factor that lowers the validity of single counts from the road for determining sex ratio is that large troops are encountered by chance. Thus, too many or too few troop males might be assigned to the census area. The larger the area, the less the error from this source. At best, a single count from the road provides a gross index of comparison between areas, not a measure of sex ratio.

The study area at Huaylarco was approximately 1000 acres. On this area at a time when the total number of resident vicuñas in bands was 125, I saw a single troop of 75 males. These males, plus 17 known band males, made up 46% of the total number of vicuñas present (200). At that time (early January), 30 new yearlings of both sexes were still members of bands. If 8 of these yearlings were males, as is not improbable, the ratio of all males to females on the area was 100:100. In general, then, the sex ratio in vicuñas is approximately balanced, but because of the difficulty of recognizing small troops and of assigning troops to a certain census area, the exact sex ratio of a population cannot easily be determined.

Doe:fawn ratio.—It is also difficult to distinguish between old juveniles and yearlings, and between yearlings and two-year olds. Therefore, no reliable ratio of breeding females to juveniles (the "doe:fawn ratio" of wildlife management workers) was obtained for vicuñas, except in the study area at Huaylarco. For that area there were 46 juveniles per 100 reproductive females (two years of age and older) in April, 1952, when nearly all young had been born.

For the 20 bands studied at Huaylarco, a summary of the age composition is given in Table 1. Each band is designated by a letter and number indicating the location of its territory. These numbers are distances in kilometers from Arequipa on the road to Puno. In Table 1, for each band the number of individuals, of yearlings, and of juveniles is tabulated by half-month periods. The numbers given are the maximum counts made on at least two days of each period, so that temporary changes in composition of bands are not included. In the few cases where individuals were known to have left one band and

TABLE 1. Composition by half-month periods of 20 bands at Huaylarco.

Band	Month 1951				Month 1952							
	November		December		January		February		March		April	
W. 139.4	.....	.....	9-0-0	9-0-0	9-0-0	10-1-0	9-0-0	10-0-1	11-0-2	1-0-0	2-0-0	2-0-0
W. 139.0	.....	.....	2-0-0	2-0-0	2-0-0	2-0-0	3-0-0	3-0-0	2-0-0	11-0-2	10-0-2	.....
S. 139.0	.....	.....	8-1-0	8-1-0	8-1-0	10-1-0	7-0-0	9-0-2	11-0-2	13-0-4	15-0-4	16-0-5
E. 139.0	11-5-0	11-5-0	10-4-0	10-4-0	10-4-0	8-0-0	6-0-0	9-0-3	10 0-4	10-0-4	10-0-4	10-0-4
E. 138.8	.....	.....	.....	.....	3-1-0	2-0-0	2-0-0	1-0-0	3-1-0	2-0-0	3-1-0	3-1-0
W. 138.6	.....	.....	.....	.....	.....	.....	1-0-0	1-0-0	1-0-0	1-0-0	1-0-0	.....
E. 138.4	6-1-0	6-1-0	6-1-0	6-1-0	6-1-0	4-0-0	2-1-0	2-1-0	2-1-0	2-1-0	2-1-0	.....
E. 138.2	5-0-0	5-0-0	5-0-0	4-0-0	3-0-0	4-1-0	4-2-0	5-3-0	5-2-0	5-2-0	5-1-0	5-1-0
W. 138.2	8-3-0	7-2-0	6-2-0	6-2-0	6-2-0	4-0-0	4-3-0	4-3-0	4-3-0	4-3-0	4-3-0	4-3-0
W. 137.7	8-3-0	10-4-0	11-5-0	11-4-0	13-5-0	11-5-0	9-2-0	8-2-0	7-1-0	7-0-0	7-0-0	7-0-0
E. 137.5	16-5-0	16-5-0	10-4-0	15-5-0	15-5-0	14-4-0	3-2-0	3-2-0	3-2-0	3-2-0	3-2-0	.....
W. 137.3	5-2-0	5-2-0	4-1-0	4-1-0	3-1-0	3-1-0	2-0-0	2-0-0	3-1-0	3-1-0	5-0-2	5-0-2
E. 137.0	4-1-0	4-1-0	4-2-0	4-1-0	4-1-0	4-1-0	4-1-0	7-1-0	12-0-4	11-0-4	11-0-4	.....
S. 135.6	.....	.....	.....	.....	.....	5-0-0	4-0-0	7-0-1	10-0-2	9-0-2	9-0-2	9-0-3
N. 134.5	10-2-0	10-2-0	8-2-0	9-1-0	9-1-0	9-1-0	11-0-0	9-0-0	20-0-4	22-0-6	23-0-8	23-0-8
N. 133.5	.....	.....	.....	.....	1-0-0	1-0-0	1-0-0	3-2-0	1-0-0	1-0-0	1-0-0	2-0-0
S. 133.2	.....	12-4-0	12-4-0	12-4-0	10-3-0	12-4-0	11-1-0	14-1-1	23-0-6	26-0-9	25-0-9	.....
N. 133.0	.....	.....	.....	.....	.....	.....	7-0-0	6-0-0	5-0-0	7-0-1	.....	.....
S. 133.0	13-4-0	15-5-0	14-5-0	14-4-0	18-5-0	15-2-0	13-0-1	13-0-1	.....	.....	.....	.....
S. 132.8	5-0-0	7-0-0	6-0-0	5-0-0	5-0-0	6-0-0	4-0-0	3-0-0	6-0-1	6-0-1	6-0-1	.....
Totals:												
All	91	108	116	119	125	124	107	119	139	144	142	86
Adult ♂♂	11	12	15	15	17	18	20	20	20	20	19	11
Non-juv. ♀♀	54	65	70	76	..	..	..	..	..	..	..	..
Adult ♀♀	..	..	..	..	78	85	74	75	83	82	79	48
1951 juveniles	26	31	31	28	..	..	..	..	..	..	..	..
1952 yearlings	..	..	..	..	30	21	12	15	11	9	8	5
1952 juveniles	..	..	..	..	..	..	1	9	25	33	36	22
Average band	8-2½-0	9-2½-0	8-2-0	8-2-0	7½-2-0	7-1-0	5½-1-0	6-1-½	7-½-1	7-½-1½	7½-½-2	8-½-2
Ratios:	Per 100 non-juvenile females				Per 100 reproductive females				(older than 1 year)			
Adult ♂♂	20	18	21	20	22	21	27	27	24	24	24	23
1951 juveniles	48	48	44	37	..	..	..	..	..	..	..	..
1952 yearlings	..	..	..	..	38	25	16	20	13	11	10	10
1952 juveniles	..	..	..	..	..	..	1	12	30	40	46	46

*Numbers indicate: total in band—old juveniles (in 1951), or yearlings (in 1952)—young juveniles (born 1952).

joined another, the loss and gain are ascribed to separate half-month periods. The totals for each sex and age class, and their proportion to 100 non-juvenile or reproductive females, are given in the lower part of the table. At Huaylarco at the end of 1951, the ratio of juveniles to older females (including yearlings) was 37 to 100 for 15 bands of known composition. Excluding four bands that did not contain juveniles, the ratio was 47 to 100. This ratio was much higher than one based on miscellaneous roadside counts of bands at various localities in southern Peru. On trips made during the period from April to September, 1951, I counted the members of 30 bands that contained juveniles. These counts gave a ratio of only 17 juveniles to 100 older females.

On some trips I counted all the vicuñas, both in bands and in troops, that I could see from the car, distinguishing juveniles from older vicuñas in the counts. These counts seemed to indicate a very low reproductive success. For example, one day in May, 1952, in a 55-mi segment of road northeast of Púquio I counted 534 vicuñas of which only 7% were juvenile. And one day in October, 1952, between Ocoruro and Pati I counted 333 vicuñas of which but 5.5% were juvenile. Assuming a balanced sex ratio, these counts give ratios of juveniles to older female vicuñas of only 14:100 and 11:100.

The first time that I drove through the Huaylarco area, in April, 1951, I counted 186 vicuñas of which approximately 6% were juvenile. Another count in October gave 176, with nearly the same proportion of young. But early in November, a more careful census indicated that 14% of 270 vicuñas in the Huaylarco area were juvenile. A few weeks later, after intensive study, I found that of the vicuñas in resident bands, 27% were juvenile. Now, including males in troops and assuming a sex ratio of 1:1, the proportion of juveniles to all vicuñas at Huaylarco at that time (December) was 18%. This percentage is much higher than any obtained by a single count. Evidently single counts give misleading results; they usually indicate a much lower percentage of juveniles

than are actually present. Such counts may be of value, nevertheless, as indexes for comparing reproductive success in the same population in different years.

POPULATION DENSITY

Maximal densities.—It is not difficult to count the vicuñas in resident bands of a given area. At Aricoma on the best sites, where good pasturage was nearly continuous, the average density of band vicuñas in winter was about 1 animal per 10 acres. At Huaylarco, in early February, 1952, just before the first young were born, the average density of band vicuñas on the study area of about 1000 acres was 9.5 acres (horizontal measurement) per animal. Some of the smallest territories supported 1 vicuña per 5 acres for a period of many weeks but such high densities were exceptional.

The number of males in a troop can also be counted easily. But because a troop wanders far, its presence on a census area is fortuitous and the proper acreage to assign it is doubtful. I made many counts, however, that included both bands and troops. For example, from the road at Huaylarco, I once (November 8, 1951) counted all the vicuñas seen in a strip 30 chains wide and 11 km long. For the total of 270 vicuñas counted, the average density was approximately 6.5 acres per animal.

These average densities are probably near the carrying capacity of the vicuña range. In the Andean highlands the grazing capacity of good sheep pasture is generally taken as 1 hectare (about 2.5 acres) per animal. Allowing for the facts that vicuña range is generally less productive than good sheep range, that a vicuña is larger than a sheep, and that livestock grazes the vicuña range during part of the year, a density of 1 vicuña per 10 acres may be all that the range can sustain permanently.

Variation in population density.—Of course if unsuitable or unclaimed ground is included in the census area estimated densities are much lower than when only territories are included. Pearson (1951:121) estimated a density of 120 acres per vicuña on a continuous area of approximately 15 sq mi at Caccachara, in southern Puno. As the topography was rough, doubtless much of the included area was not pastured by vicuñas. In arid regions where green food is scant population densities may be much lower than those illustrated. In the Antofagasta study area the population density was estimated at 50 per 100 sq mi—more than 1000 acres per vicuña. Probably similar low densities predominate in most of the vicuña range in Chile, Argentina, and southern Bolivia.

From one area to another the concentration of vicuñas differs widely. I counted 428 vicuñas while driving 48 miles of the road between Chalhuanca and Púquio, Peru, in May, 1952. Considering the area searched, the density was about 35 acres per animal, including juveniles. In driving from Ocoruro southward to Pati in October, 1951, I counted 309 vicuñas in a strip 50 mi long and 0.5 mi wide. The average density was 50 acres per animal, but much of this strip was unsuitable for vicuñas. In one 7-mi segment of the strip the density was 20 acres per vicuña. Driving from Crucero to Poto in the winter of 1951, I saw an average of less than 2 vicuñas per mile along the two most favorable stretches, 14 and 25 mi in length. The density there was in the neighborhood of 160 acres per animal. For large areas where there are many vicuñas, the average density in southern Peru is estimated to be less than 50 acres per animal.

Counts from an automobile without regard to the width of strip surveyed give a gross index of vicuña population densities. Using this method I saw an average of 15 per mi while driving 5 mi across a tola flat at Chilliculco (Puno, Peru) on May 1, 1951; an average of 4.5 per mi while driving 18 mi across semi-desert pampas near Lake Loriscota on May 3, 1951; and 5.9 per mi while driving 19.5 mi from Imata to Pati on January 27, 1952. Such counts may give misleading results unless standardized as to length of run, time of day, and other factors. Unknown previous disturbances, such as the passing of a dog, can greatly influence the number of vicuñas in an area.

For Peru alone the total number of vicuñas has been stated to be approximately 1,000,000 (Cardozo 1954:194, from other source). In my opinion this figure is much too high. The perimeter of the vicuña range in Peru (Fig. 3) includes about 38000 sq mi, but mountain peaks, barren soils, and human activity within this region make an estimated half of it unsuitable for vicuñas. Thus, in Peru there may be only 19000 sq mi, about 12,000,000 acres, of land inhabited by vicuñas. If there were 1,000,000 vicuñas in Peru the average density would be about 12 acres per animal. But such high densities exist only at favored and restricted sites. On the basis of a more probable average density of 50 acres per vicuña, there are slightly less than 250,000 vicuñas in Peru.

The ground included in the outline of the entire range of the vicuña (Fig. 3) has an area of approximately 100,000 sq mi, two-thirds of the area of California. If half of this ground is occupied by vicuñas, they utilize 32,000,000 acres. About 60% of the vicuña range is in the dry and salty zone south of the latitude of Salar Uyuni, Bolivia (latitude 20° S), where average population densities are thought to be low, perhaps 1000 acres per vicuña. On the basis of these estimates, there are approximately 400,000 vicuñas in all, more than half of them being in Peru.

MORTALITY

Death rate.—At the end of the season of birth many adult females at Huaylarco were without young. Yet a few months earlier nearly all females except yearlings appeared to be pregnant. The ratio of only 46 juveniles per 100 reproductive females in April (Table 1) suggests that about half of the young perished during the late fetal or infant stage. The cause of this apparently high mortality was not discovered. Probably productivity was even less at other localities, where bands were smaller and the

proportion of young to adults was lower than at Huaylarco.

In the wild, dogs, Indians, and condors probably kill many newborn young. But on the vicuña ranch at Calacala, where these predators are of minor importance and stillbirths are rare, reproductive success is equally low. There, 200 breeding females produce about 70 juveniles, according to Sr. Paredes. He blamed foxes for the high loss of young. I suspect that, in some years or under poor range conditions, fertility may be low among the younger breeding females (two-year-olds). Future wildlife workers might well concentrate on this problem of reproductive success.

In the bands at Huaylarco in April, the proportion of juveniles to yearlings was 46 to 10. If these figures are typical of all years, there is a loss from bands of about ¾ of the juveniles during their first year of life. This loss is caused not only by death, however, but by the departure of all male and many female yearlings from the bands. Thus, the mortality rate of juveniles is difficult to judge. Comparison of the ratio of juveniles to band adults in early April (29%) with the ratio in late November (25%) suggests that mortality in juveniles between 2 and 7 months of age is low.

Theoretically, in a stable population annual mortality in vicuñas older than yearlings would be equal to the number of new yearlings. On the basis of figures for Huaylarco, this number would be about 38 per 100 reproductive females, in January, or 17% of all vicuñas older than yearlings (assuming a 1:1 sex ratio). One should not trust these figures too far, because the basic assumptions that the population is stable and that the data for one year are typical of all might be wrong. For significant analysis of age composition and mortality it is necessary to have accurate counts of one population, by age classes and including troop males, for a period of several years.

Disease and injury.—To determine the causes of mortality in any wild population is difficult. Fresh carcasses are hard to find, for dogs, foxes, condors, caracaras, and other carnivorous animals may consume the body of an adult vicuña within a week, and of a juvenile within a day. Hunters who kill vicuñas leave little evidence behind.

In the higher parts of their range, vicuñas may have few parasites. None of the vicuñas that I studied appeared to be suffering from disease. I made a gross examination of three vicuñas that had been shot, but I found no abnormalities, parasitic worms, or ectoparasites. Pearson (1951:167) tells of a pregnant female that died in the wild "apparently from an intestinal inflammation." Allen (1942:412) reports that lungworm, scab, and flukes have been found in vicuñas, but he does not state whether these were wild animals. Romero (1927:151) mentions mange and itch ("la sarna") as lamoid diseases that probably spread to vicuñas. Garcilaso de la Vega (1871:378) tells of an outbreak of the itch in llamas in the year 1544. He relates that the disease spread to vicuñas, but implies that it did not have a serious effect on the population.

James Mitchell, for many years a veterinarian on Peruvian haciendas grazed by llamas, alpacas, sheep, and vicuñas, told me that all of these animals were infected with scab, and many with tapeworm cysts in the liver and other organs. Another veterinarian of central Peru, D. F. Watson, wrote me (1954) that vicuñas found dead on sheep ranches usually have scabies and many internal parasites. Apparently, then, where vicuñas graze sheep pastures they may become heavily infected with parasites. Possibly infection follows the weakening of the animal from other cause. Tschudi (1844-46:232-233) relates that sometimes a single vicuña would allow itself to be approached, and it could be caught by a horseman with lasso or bolas. The Indians told him that these animals were tame because they were infected with worms. Some carcasses examined by Tschudi were found to have cysts of intestinal worms in the pancreas and liver, and roundworms in the colon. Evidently, under certain conditions parasitism may reduce the vitality of vicuñas.

In a four-month period at Huaylarco, I noted 10 injured vicuñas. About half of these had a lame or broken leg. Some wounds were surely made by gunshots. Others were probably caused by collisions with automobiles, or by falls on rough ground. Nearly all the injured vicuñas were males and, because an injured male cannot well defend a territory, most of them were members of troops. One adult male in a troop appeared to be well fed and grazed normally although one of its legs, broken just above the ankle, dangled limply.

The family male of one band which I was studying became seriously injured. I found him lying close beside the road. Half an hour later he rose, with great effort. For several minutes he remained at that spot, sometimes raising or lowering his head very slowly. Then he walked a short distance, very unsteadily, for one leg was unable to bear his weight, and again he lay down. Half an hour later he got up again, faltered up a gentle slope, crossed the road, drank from a puddle, nibbled some grass, and then lay down, almost tumbling sideways in the act. When I walked toward him he allowed approach to a distance of 50 yards before he rose and trudged away. Three days later he could walk fairly well.

In the puna, there is much snow and hail during the season of birth. Severe storms might cause a heavy loss of juveniles, on occasions. At Calacala young vicuñas, as well as lambs, are sometimes found dead after snowstorms.

Life span.—A female vicuña born at the New York Zoological Park in 1904 lived for 24 years (R. M. McClung, letter, 1953). This is the greatest longevity known for a vicuña. One of 3 still living in that zoo is at least 15 years old (a female, purchased in 1940). Many other zoo specimens have survived more than 10 years, and as experience is apparently of great survival value in the wild, some wild vicuñas

may live at least 10 years, though the average life span is doubtless much less.

GENERAL ACTIVITIES AND REACTIONS

To anyone who watches vicuñas for a few hours it soon becomes obvious that they remain in discrete groups whose principal activities are grazing and resting. From time to time individuals void or scratch. When one walks too close to another, the latter may spit at it. And if the observer approaches the vicuñas, one of them gives a call and the group runs off.

RESTING IN DAYLIGHT

Lying down.—A vicuña spends more than half of its life lying belly down with its legs tucked under its body. In this prone position the wrists and ankles are flexed double and the heels nearly touch each other. This is the characteristic posture for resting and sleeping, for females during copulation, for newborn young before they can stand (Fig. 10), and for sick and dying vicuñas. In play-fights, lying prone is often the final defensive action. On occasions while lying prone a vicuña extends one wrist, then the other, so that the forefeet lie close together in front of its chest. A few minutes later it doubles the feet under its chest again. Sometimes a resting vicuña lays its head on the ground, perhaps on a rock or mound. Commonly, in this pose only the chin touches the ground, the neck being extended far forward and arched a few inches above the ground surface. Even newborn young may rest thus.

FIG. 10. Vicuñas are born in the wet season, when snow or hail falls nearly every day. This infant, about 20 minutes old, lies prone in typical camel fashion. Huaylarco, Arequipa; March 4, 1952.

The prone position is warm, for the slender legs are exposed as little as possible and the long brisket hairs protect the forelegs from cold. That the pose is steady is attested by the observation that, for several days after death the body of one vicuña remained in the characteristic prone position. One native belief is that a vicuña sleeps with its throat behind its forefeet so as to guard against the attacks of foxes.

As a vicuña prepares to lie prone, it noses the ground and makes two or three false starts by flexing one foreleg. Then it doubles one wrist, then the other, placing the two knuckles down side by side. By flexing the hindlegs, it lowers its knees to the ground. Next, as the elbows drop and the wrists slide forward, the chest descends. Lastly the hindfeet shuffle forward so that the heels bear on the ground. The whole process may be performed in slow jerky fashion, or too rapidly for the observation of details. Apparently all the members of the camel family lie prone in approximately this manner. Rising is normally rapid. The trunk heaves forward as the straightening hindlegs raise the posterior body. Then one wrist is lifted, the forefoot planted, and the other foreleg likewise extended.

Vicuñas prefer to rest on dry bare soil, but sometimes they lie prone on mud or snow. When a group is resting the spacing and orientation of individuals is irregular. Frequently the male of a band lies at a short distance from his family, and the juveniles may rest together a short distance from the adults, but the group does not assume a formation of any seemingly defensive advantage. Juveniles often graze while lying prone, but adults rarely do. All, however, chew cud while resting. Upon becoming alert a prone vicuña stops chewing, raises its ears, and elevates its head a few inches. Then, as alarm subsides, it resumes chewing and lowers its ears and head. Prone

TABLE 2. Schedule of daylight resting and voiding for one band[a].

Band member	Male	Female 1	Female 2	Female 3
Duration of rest periods[b]	6:00- 6:12 6:38- 6:41 7:28- 7:32 7:43- 8:06 8:50- 9:17 9:39-10:02 11:55-12:43 1:03- 1:28 3:26- 3:55	6:00- 6:23 7:22- 7:32 9:59-10:18 11:32-11:52 12:28-12:43 1:12- 1:32	6:00- 6:15 6:22- 6:31 9:07- 9:17 9:52-10:01 10:02-11:01 12:33-12:42 3:33- 3:58	6:00- 6:05 6:15- 6:25 7:23- 7:35 8:28- 8:47 10:18-10:48 12:00-12:43 2:22- 2:35
No. periods	9	6	7	7
Total minutes	194	107	137	132
Ave. duration	22	18	20	19
Range (min.)	3 to 48	10 to 23	9 to 59	5 to 43
Time of voiding	6:16 6:52 8:18 10:28 1:35 2:19 3:15 4:15 4:54	6:23 10:52 2:11 3:20	6:21 11:04 12:12 3:05 3:20	6:25 11:04 3:20
Voidings	9	4	5	3
Interval between voidings:				
minimum	36 min.	1 h. 09 m.	15 min.	4 h. 16 m.
maximum	3 h. 07 m.	4 h. 29 m.	4 h. 43 m.	4 h. 40 m.

[a] Band *B*, Aricoma, August 2, 1951.
[b] Only periods of more than 3 minutes are included.

vicuñas occasionally yawn with ears back, muzzle raised high, and mouth held wide open for a second or two.

When the sky is heavily overcast during the day vicuñas may lie prone for long periods, but in this weather they seldom lie down on their sides. It was often observed that soon after sunshine broke through the clouds several prone vicuñas lay down on their sides, as if sunlight stimulated the action. Lying on the side is an unwatchful position, seldom maintained more than 15 minutes at a time. While the vicuña lies on its side, its neck and head may be held up or they may lie sideways on the ground. The flexed legs usually sprawl, though the forelegs may be tucked under the chest. On hillsides vicuñas lie with body horizontal across the slope, legs downhill.

Resting schedule.—At Aricoma, most of my observations were of two bands called A and B. The resting schedule of the members of band B for 12 hours of daylight is given in Table 2. These data show that each animal took 6-9 rests for an average period of about 20 minutes, the longest periods being about one hour. On the average, each vicuña rested nearly 2.5 hours, about 20% of the 12-hr period. After 4:00 p.m. these vicuñas did not rest during daylight. In fact, only one third of the 29 rest periods started after 12 noon. In this example, the male rested half again more than the average for females. If there had been many transgressions of his territory by other vicuñas, the resident male would have had less time for rest than the females. Of the intervals between rests 40% were over one hour in length, the longest being 2 hours and 50 minutes.

Another day, during the 5 hours preceding noon I watched a band of 6 members. There occurred 15 individual rest periods of 10-70 minutes each, not counting periods of less than 3 minutes. The average per animal was 2.5 rest periods, each 33 minutes in length.

The frequency and length of daytime rest periods are irregular. The amount of time spent in rest is greater at some localities than others, presumably because less time is needed to ingest sufficient food at the former sites. But in general, vicuñas in bands rest for a period of one-quarter to one-half hour at intervals of 1-2.5 hours. In Fig. 11, a bar graph of the data of Table 2 without regard to individual identity, a tendency for the group to rest at intervals of about 2 hours is apparent.

In male troops too, there is a tendency for a large proportion of the members to lie down at intervals of about 2 hours during the day, the first rest period usually occurring about 8:00 a.m. For example, in one troop of 30 males, 20 were lying down at 7:55 a.m., 27 at 9:30 a.m., and 14 at noon, fewer being down in the intervals between these times. Resting periods of a troop are not clear-cut, however, because the members lie down or arise a few at a time, not all at once. In one troop of 19 undisturbed males 9 were lying down at 8:30 a.m., then 15 by 8:44, 16 by 8:55, and 17 by 9:05. But by 9:18, 11 males had risen, and all were up 4 minutes later. The rest of troop males is often interrupted by the attacks of family males. But soon after the attack is withdrawn many members of the troop lie down, as if a rest were overdue. Among the members of troops the action of lying down is moderately contagious; if one lies down others soon follow suit.

Reaction to storms.—Vicuñas take little notice of falling rain. They allow snow to accumulate on their backs and necks, without shaking it off. And they do not hesitate to walk in snow when it is several inches deep. If the wind is moderate, grazing continues in snow, hard rain, or light hail. But when these are driven nearly horizontally by the wind, many vicuñas lie prone facing downwind.

Before lying down, the members of a group may run a short distance, often from a flat to the base of a hill as if to reach a sheltered spot, and they gather close together. While lying prone during the storm the vicuñas in a group may be close together or scattered. One band of 11 lay down within a space of 15 x 5 yds. But the members of another large band lay down in approximate file, strung out for a distance of 50 yds, no more than 2 vicuñas lying together.

All members of a band may lie prone within a minute, and sometimes within half a minute, after the start of hard hail. In one observation, all 18 males of a troop quickly lay down as hail commenced. Then when the hail increased in intensity a few vicuñas rose, walked forward, and lay down again; others did likewise. The group thus grew more compact, so that the sides of some vicuñas nearly touched

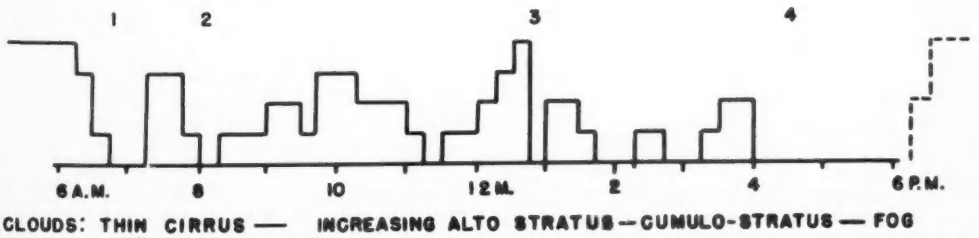

FIG. 11. Daylight resting periods of a band of 4 members. Height of bars indicates maximum number of vicuñas resting at one time during each quarter-hour period. Numbers above bars indicate events as follows: (1) another group neared; (2) band walked a quarter-mile; (3) mild disturbance by man; (4) light snowfall.

others. Doubtless, within a compact group vicuñas are somewhat protected from wind and hail by the bodies of their fellows. While the hail falls the prone vicuñas hold their ears back horizontally, heads lowered to the level of their backs, and they remain nearly motionless even though their heads and necks become caked with ice.

How long will vicuñas remain prone during a hailstorm? In one observation, all 10 members of a band remained down for a period of an hour. Then the hail turned to wind-driven snow and 3 vicuñas rose and grazed, but the other 7 stayed prone a half hour longer. Vicuñas differ in their readiness to lie down when a storm commences, or to rise after it is over. The last member of a group to lie prone is often the first to rise and graze when the hail abates. It may be the hungry individuals which are least inclined to remain inactive for long. Frequently one member of a band, perhaps usually the male, continues to graze while the others lie down. Sometimes all members of one group remain down while a band close by continues to graze. When finally the hail stops or turns to rain, the prone vicuñas rise a few at a time. Upon rising, some shake off part of the accumulated ice. Several minutes after the storm all are up and grazing.

RESTING AT NIGHT

Characteristically, bands of vicuñas spend the night resting on their daylight feeding grounds. On many of the territories that I studied, a lower flat area was favored for late afternoon grazing. From these flats the vicuñas walked uphill shortly after sunset in order to bed down. On many occasions I censused bands of vicuñas in the late afternoon as they grazed on the lower parts of their territories, and then again early in the next morning when they were still resting on the higher slopes.

Time of bedding down.—The time that vicuñas bed down was found to be fairly regular; about an hour after sunset at Aricoma in winter, and a half hour after sunset at Huaylarco in summer. For example, here is an observation made at Aricoma one evening in August. At 5:05 p.m. the sun set at the site where the 10 members of bands A and B were grazing. At 6:03 p.m. 3 members of band A were lying down. Seven minutes later, with the Southern Cross visible in the sky, only 2 of the 10 vicuñas remained standing. Vicuñas normally bed down by the time that bright planets become visible to the naked eye. Evidently the time when foraging stops depends upon light intensity. In an observation made one evening in July, the 7 members of a band were diligently grazing on a flat at sunset, 5:03 p.m. The band started uphill to bed down at 5:30 p.m. At that time the light from the zenith was 1.0 ft-candle and from the brightest point of the sky 3.2 ft-candles, as measured with an ordinary photoelectric exposure meter. Variations in the schedule of bedding down are evidently caused by hunger, the shadow of mountains, and clouds. In a few observations in which heavy clouds obscured the setting sun, bands of vicuñas bedded down about one-quarter hour earlier than on clear days.

As twilight is short in the tropics, all the vicuñas in an area usually bed down within a period of less than half an hour. Bedding down is delayed little, or not at all, by bright moonlight. One evening in July, I watched a band of 5 members which was still grazing one hour after sunset, casting shadows by the light of the full moon. But all were lying prone by 6:25 p.m.

On occasions when a band is excited, its members may be active when darkness precludes observation. In early January, I was observing a band of 18 grazing vicuñas when the sun set behind clouds on the horizon at 5:55 p.m. A quarter hour later the male of the band attacked a nearby troop. Then, at 6:37 p.m., when Orion was visible and the light from the brightest point in the sky was only .4 ft-candles, I noted that 3 members of the band were lying down. Soon 8 were down. But about 10 minutes later I saw by a flash of my spotlight that half of the band was still up, and several vicunas were running about.

Site of bedding down.—Vicuñas usually rest for the night on dry sites of moderate slope, well downhill from ridgetops. Many bands normally bed on upper slopes of their territories, but downhill from still higher barren slopes. These bedding sites are relatively free from disturbance because there are seldom vicuñas on the unclaimed ground upslope, and because livestock, men, and carnivores usually travel the lower slopes and canyon bottoms. With moderate consistency, the same general sites are used repeatedly for bedding down. One band of 10 members bedded down within 50 yds of the same spot on 3 consecutive nights.

Bands that inhabit flat territories may remain all night far from slopes or cover. For example, one evening at 6:00 p.m. I saw two bands, totaling 21 adult and 10 juvenile vicuñas, lying prone on a wide pampa, 200 yds from the nearest slope. At 5:30 a.m. the following morning they were still lying at the same site. Cover is not avoided when present, however, for one band often bedded down near a certain group of boulders a few feet high. No definite bedding depressions, such as those formed by deer, are made by vicuñas.

Although bands normally bed down on their own territories, they sometimes move to unclaimed ground to spend the night. Perhaps this move is made only when the band is disturbed on its territory in the evening. On one occasion, at dawn I discovered a band resting on a narrow trail across a shale slide, 200 yds uphill from the nearest grassland. It is probable that the group had been disturbed by horses, which grazed in the vicinity. On another occasion, I watched a large band graze on its flat territory near the foot of a steep barren ridge for a long period, until 5:30 p.m. Then the vicuñas started to walk up the slope, out of their territory. Twenty minutes later all had reached the crest and were walking away, farther from their territory. On this occasion I did not detect any cause for alarm. In a similar observation, a

band grazed on a pampa until half an hour after sunset, and then walked to the foot of a slope 300 yds distant and out of their territory. They ascended to a barren hilltop and walked on over it. In this instance, the vicuñas might have been slightly alarmed by my car, for a few days later the same band remained all night on the pampa in their territory, some adults lying down only 20 minutes after sunset. I suspect that vicuñas may tolerate during daylight some mild disturbance, such as the presence of a car, which they will not tolerate in the evening, when they commence to bed down. In studies of the California condor, I noted such a lowering of the threshold of tolerance for disturbance at the time that the birds commenced to roost for the night.

Activity at night.—Vicuñas rest nearly all night, it seems, usually lying prone. As when resting in daylight, they face various directions in no particular formation. Members of the same band may lie 3-15 yds apart, and a large band may bed down within an area 30 yds in diameter. The band male tends to lie a short distance from his family. Perhaps he usually lies lower on the slope, for on two occasions when I alarmed a band mildly at night only the downhill member rose and gave the alarm trill. By day it is typically the male which acts thus. The members of a troop also bed down together. At dawn one morning I noted a troop of 24 males lying on a hillside, spread a distance of 100 yds up and down a slope. A cluster of 7 lay 25 yds uphill from a group of 6, and the others were scattered farther uphill.

Bands often move a short distance during the night, for in the early morning they are seldom found at the exact sites where the first few members lay down the previous evening. For example, one evening 3 members of a large band lay prone at a certain spot at 6:05 p.m. At 4:20 a.m. the next morning the group was lying 200 yds distant from that spot. Movements of short distance during the night may be incident to voiding or to nursing young. Long moves are probably caused by disturbance. On a few occasions, I observed that a familiar band was not on its territory at dawn although it had bedded down there the previous evening. Presumably there had been a disturbance at night, for on each occasion the band returned to its territory soon after sunrise.

Rising in the morning.—Sunlight, evidently, is the principal factor that determines the time of rising in the morning. Yet, vicuñas do not seek sunshine from shadow. At Aricoma I often started watching the activities of family bands in the early morning, before the first vicuñas had risen. Typically, the earliest risers stood up soon after sunshine struck the highest peaks, half an hour before it struck the bedding site, and the latest risers got up a few minutes after the rays of the sun struck them. An example of the rising of a band at Aricoma is as follows: 6:00 a.m., all 4 members of band B still prone. 6:05, immature female stood, grazed. 6:12, male rose, grazed. 6:15, immature female lay prone; one adult female rose. 6:21, adult female lay prone again; second adult female rose. 6:25, immature female rose again. 6:31, one minute after sunshine struck group, first female rose again; all four were up. Here, as in most observations, the interval of time from the rising of the first to the last member of a large group was about half an hour.

Within this interval there is much variation in the time of rising of two bands in the same area, or of the same band on successive days. In one observation at Aricoma, 4 members of band B were standing at 6:05 a.m., but all 6 members of A were still lying down. Two members of A stood briefly, then again lay prone. At 6:30 a.m. sunshine first struck this band. All members were up five minutes later. The following morning all 11 members of these two bands were on their feet nearly half an hour earlier, at 6:10 a.m.

The observed times of rising at Aricoma in winter were about 1.5 hours later than at Huaylarco in summer. Part of this difference was due to the difference in season, and part to the fact that surrounding peaks blocked early sunshine at Aricoma. But in addition, to satisfy their hunger vicuñas apparently had to graze for more hours at Huaylarco than at Aricoma, because forage was less abundant at the former site. Vicuñas also spent less time in resting during the day at Huaylarco than at Aricoma.

Observations at Huaylarco indicated that during a period of about 4 months, from early summer to mid-autumn, the average time of morning rising became later by about 1 hour. For approximately 30 band vicuñas on a certain pampa, the usual time that all were first on their feet was about 5:00 a.m. in December and 6:00 a.m. in March. This difference was probably due to changing pasture conditions and changing demands of young, rather than to any change in the position of the sun.

The time of rising may be delayed by cloudy weather. In an observation made one morning in January, when the sky was overcast and snow was falling lightly, only one vicuña of a group of 12 had risen by 6:30 a.m., an hour and a half after the usual rising time. Rising in the morning takes place at much greater light intensities than bedding down for the night. Before they rise in the morning vicuñas are clearly visible at long distance, yet they often continue to graze in the evening when human sight fails.

Although I found no significant difference due to sex or age in the time of rising in the morning, some observations suggested that troops tend to start foraging earlier than bands. Troops would profit from early grazing, for they are subject to many disturbances that interrupt feeding during the day.

A mannerism that often occurs shortly after first rising in the morning, but rarely at other times, is a cat-like stretch. In stretching, a vicuña leans forward with hindlegs slanting far back, extends its neck forward and down so that the chin nearly touches the ground, and holds this pose for a few seconds.

VOIDING

Dung piles.—Lamoids defecate and urinate on com-

munal dung piles. Vicuñas of both sexes and all ages use the same piles, normally visiting the closest at hand. Displaced bands freely use dung piles that are situated on the territories of other bands. Alpacas and llamas use the same piles that are used by vicuñas. One typical large pile was 1 ft thick at the center and 5 yds in diameter. The center third of the surface was solid feces, the peripheral two-thirds carpeted with short nettles and other plants. Average pellets are 11-15 mm long, a third less in diameter, and irregularly ellipsoid in shape. Dry pellets are firm but can be mashed by a hard pinch of the fingers.

On flat ground where there are many vicuñas the regularity of the spacing of dung piles, about 50 yds apart, is striking. On poor range the piles are widely spaced, perhaps only one, a mere sprinkling of pellets, occurring every quarter mile near frequented pathways. The spacing, size, and freshness of dung piles could be useful in estimating the abundance of vicuñas on different sites, providing allowance were made for the contributions of alpacas and llamas.

Manner of voiding.—The male vicuña typically defecates in the following manner: He walks to a dung pile, sometimes as far as 50 yds distant, raising his tail high when he reaches a point a few yards from it. Upon reaching the pile he noses it for several seconds. Next he puts his forefeet atop the pile and treads them alternately a number of times, at a rate of about two steps per second. Then he turns about so that his anal region is downslope and spreads his hindfeet wide. In the defecation posture the head is lightly lowered, the ears are horizontal, and the tail points out or slants upward (Fig. 9). During a period of 5-10 seconds, as many as 7 fist-sized clumps of pellets fall.

Urination starts as defecation stops. The male urinates for a period of about half a minute, the fine urine stream passing posteriorly between the backs of his knees and falling behind his ankles. The stream surges and his extended tail pulses up and down simultaneously, apparently in time with the beating of his heart (130-150 pulsations per min). A male may remain in the voiding stance for 1.5 minutes. Then he walks away from the dung pile and lowers his tail slowly. Immediately after voiding a vicuña sometimes turns about, noses and treads the pile, turns once more, and again voids. Walking in water stimulates urination (Fig. 4). As one troop of 20 males crossed a stream, 7 stopped and urinated in the water.

Females differ from males in the manner of urination. After defecation, at the start of urination, the female lowers her hind quarters about 4 in. Then the angle at her heel joint is about 110°, as contrasted to about 160° in the male. Also the urine stream of the female is much thicker than that of the male, and it flows for a period about half as long. The stream of the female spurts strongly for approximately one second at irregular intervals of about a second. Opportunity for the distant observer to determine the sex of individual vicuñas is greatest when they void. Not only can differences in the manner of urination be observed, but when the tail is raised the bulging testes and black-tipped penis of the male may sometimes be seen.

Juveniles void in the manner of adults of the same sex. While standing alongside its mother, a juvenile but 40 hours old spread its hindlegs as if to defecate, but no feces fell. The youngest one actually seen to defecate was about 4 days old. In the adult manner, this infant nosed a dung pile, turned around, and voided a single pellet. Another, 7 days old, extruded but 2 pellets. In the few days before young commence to graze they probably have little digestive waste to eliminate.

Frequency.—The interval between successive defecations may be as long as 5 hours. Adult males void more frequently than females—perhaps twice as often. This difference is probably due to the fact that males react more strongly than females to the scent or sight of dung piles. One male defecated 3 times during a period of 10 minutes, then again 10 minutes later. For a band which I watched for 12 hours during daylight, the average interval between defecations was about 3 hours for the females, and half as long for the male (Table 2). Voiding is infrequent late in the day, when vicuñas are absorbed in feeding.

Although there is great irregularity in the intervals between defecations, all members of a band are fairly sure to defecate within a period of half an hour after first rising in the morning. Yet, vicuñas are in no hurry to void upon rising; 20 minutes may elapse between the time that the first member of a band rises and the time that the first defecates. An example of the schedule of the first voidings of the day by 4 members of a band follows: 6:00 a.m., all prone. 6:05, immature female rose. 6:12, male rose. 6:15, adult female rose. 6:16, male defecated. 6:21, adult female defecated. 6:22, other adult female rose, defecated. 6:25, immature female defecated; male defecated again.

As the amount of feces dropped in the first evacuation of the day is not greater than subsequently, and as vicuñas do not defecate at once upon rising, it is probable that they void from time to time during the night. Shortly after dark on a moonlight night, one member of a band which had been bedded down for half an hour was seen to rise, walk to a pile, defecate, return to its bedding place, and lie down.

All visits to dung piles are not for the relief of rectal pressure. Commonly a male, and sometimes a female, will defecate on two separate piles within a few minutes. When walking near a dung pile, and especially when nosing it, a vicuña of either sex may raise its tail and even void a few pellets. Probably the scent of dung stimulates defecation, but this action also appears to be contagious. On occasions, many or all members of a band defecate within a period of a few minutes. Several vicuñas in turn may void on a pile, one waiting nearby until another leaves it. Sometimes two or more vicuñas void on a pile at the same time. In all, the attraction of a dung pile to passing vicuñas is great. As one band of 5

members filed past a pile the first two stopped and voided, the third passed by, the fourth nosed the pile, and the trailing male voided on it. Even when a troop of males is retreating under attack, several members may pause at a dung pile and add to it. When an adult male is running to challenge another, or as he returns from an encounter, he usually stops at one or more dung piles and defecates.

SPITTING

In popular accounts the spitting of lamoids has been publicized as a hose-like stream of vile-smelling saliva, accurately directed at the white of the eye of an enemy. Some books state that the whole contents of the stomach may be thrown at the attacker. But the spitting of vicuñas is no more than a quick forceful expulsion of air, which incidentally sprays out saliva and small fragments of whatever masticated food is in the mouth. When I scratched the neck of a domestic vicuña, it spat at my chest. So sudden was the blast that I was startled, but only a few bits of grass and dewlike droplets of clear liquid clung to my sweater. Often I heard the sudden *puff* of spitting at a distance of 100 yds. At some distance the blast is normally invisible, but on a cold day the warm moist expelled air may condense as a cone of fog.

Spitting or blowing is an act that shows "displeasure" insufficient to merit a kick. The spitter holds its muzzle tilted up and its ears far back. At least to a man, the throwing back of the ears serves as a warning that a blast might follow. The vicuña receiving the blast stands stiffly with its head turned away from the other and its ears back. Sometimes the two remain poised for more than half a minute. A kick or a chase of a few steps often follows a blowing attack. Occasionally an annoyed vicuña spits forward into the air while the disturber stands behind it. Spitting encounters are common between females of a band, between band females and juveniles, and between troop males, but rare between an adult male and female, or two family males.

GROOMING

Rolling.—A vicuña dusts its fleece and scratches its neck, side, and legs, by rolling vigorously on the ground (Fig. 12). Usually before rolling the animal noses the ground and paws the soil a few times. Then it drops to the knuckles of its wrists, flops down onto its side, and thrashes a few times. In each thrash the forelegs are flung forward, the hindlegs backward, and the head, neck, and tail tossed dorsally, all at once. Then the vicuña flops over onto its other side and thrashes again. In one observation, a vicuña repeated, 5 times in quick succession, the whole act of lying down, rolling, and standing up. Often a vicuña remains prone for several minutes after rolling, or it rolls just before standing up. Even juveniles a few days old may roll energetically.

Vicuñas prefer to roll in dust, but commonly they roll on dry turf, and occasionally on bunch grass or tola. Rarely do they roll on mud, or when their wool

FIG. 12. In rolling on bare ground a vicuña thrashes its neck and legs forward and backward. This female gave birth a few days later. Huaylarco, Arequipa; February 27, 1952.

is wet from rain or bathing. At Huaylarco, they often rolled in shallow pits of dust about 6 ft in diameter. These pits were apparently formed by the rolling of llamas and alpacas, however, more than by the actions of vicuñas. The flat-bottomed dusty beds of dry pools are also choice sites for rolling. As a group of vicuñas walks across such a dry pool, several members may lie down and roll in the dust. But rolling is also a means of scratching, and vicuñas roll their backs hard against the uphill banks of dust pits.

The action of rolling is contagious, even between bands. Within a period of a few minutes all members of a band may roll. In one troop of 19 males, seven rolled at the same time. In bands of 12 and 15 members, 40 yds apart, 5 of each band rolled simultaneously. Soon after one vicuña walks to a dust bowl and rolls, others may follow suit.

Members of male troops may roll even though a challenging family male stands but 50 yds distant. In fact, troop males and displaced bands tend to roll soon after being chased by a territorial male, as if rolling were a sign of relief from tension. The same explanation might account for the fact that a family male sometimes rolls immediately after chasing other vicuñas, and that vicuñas often roll after watching a fox.

Scratching and shaking.—Vicuñas scratch themselves many times a day. The tip of one hind toe is delicately used to scratch from 10-20 strokes at various parts of the forelegs, shoulders, ribs, or lowered head. In attempting to scratch, juveniles a few days old sometimes lose balance. A common action of both adults and young is the rubbing up and down of the rear surface of one metatarsus with the anterior surface of the ankle of the other hindleg. Possibly this action rubs loose scales from the external metatarsal gland. The rapidly nibbling incisors are also versatile in scratching the skin, or in cleaning the wool of the back, legs, belly, buttocks, and other parts. Groom-

ing with the mouth often continues for 3 minutes, 10-20 nibbles being taken at each spot.

While lying down a vicuña may rub its neck and head on bare soil, rock, grass, or shrubs. Occasionally one pauses in walking and brushes its head or neck back and forth through a bush or a tuft of grass. At other times, especially just before rolling, a vicuña lowers its neck and one shoulder to the ground, then scrapes them along the surface or through a bush by pushing a few steps forward with the hindlegs.

Commonly after scratching, rolling, or bathing, a vicuña shakes its head. In addition, after rolling or bathing it may shake its body with a vigorous lateral twisting motion. Sometimes the ears are waggled back and forth independently to shake off a snowflake or perhaps a fly, and the tail is occasionally switched.

COMMUNICATION

Voice.—When a band is approached by a man, dog, alien vicuña, or other disturber, an alarm trill is given by the resident male. In typical form this call consists of approximately 5 separate notes, delivered in a period of about 4 seconds. The first note is often near middle C, and each succeeding note starts a tone lower than the one before it. Each chirp slurs down two or three full tones and diminishes in volume. Commonly the final note slurs down very slowly and trails off into inaudibility. A diagram of the call is given in Fig. 13.

FIG. 13. Diagram of the alarm trill of a male vicuña. Several whistling notes are given in rapid succession, each starting a tone lower than the one before and slurring down, diminishing in volume.

There are many variations in the trill. On occasions the sound is a pure whistle. Again it is thin, stringy, squeaky, screeching, hoarse, or rasping, with no musical quality. Perhaps only 2 notes can be heard, or as many as 10. In some variations the first few notes, or all of them, are monotone, or the descending steps are half tones. No notes, or only the terminal one, may slur down and fade in volume. The delivery may be fast (more than 2 chirps per sec) or slow and mournful (one per sec). In some observations, I noted the call as *chee chee choo choo choo*, or as a series of *chucks, chirts,* or *cheets.* The trill often reminded me of the sound made by rubbing a cork back and forth on glass. The whole call may be repeated again and again. Probably there are differences correlated with sex and age.

When giving the alarm trill a male does not vary his facial expression or open his mouth, but with the sounding of each note his nostrils dilate and his abdomen contracts. It appeared to me that the male trilled while forcing air out through his nostrils.

The calling male faces the source of alarm and vicuñas close by then turn and face him, unless they see the disturber. Immature troop males call, but less readily than family males. Female and young vicuñas rarely trill, but they can do so. Once as I walked near 2 juveniles about 8 months old they squealed at me in different pitches.

The effect of the alarm call on other vicuñas reaches far beyond the family of the male, but if the trill is heard in the distance grazing vicuñas may respond only by raising their heads for a moment. Yet, in one observation, persistent calling at me by an adult male evidently alarmed a distant band and caused it to move a quarter of a mile away. Alpaca-vicuña hybrids at Calacala were heard to trill in about the same manner as vicuñas, but alpacas and llamas were not heard to call. Guanacos have a call similar to that of the vicuña, it is said.

The fact that vicuñas have large ears suggests that their sense of hearing is well developed, but my observations in daylight indicated that the hearing of vicuñas is no more acute than that of man. In daylight good hearing would seem to be of much less value to a vicuña than good sight, but at night the most important sense for detecting predators might be hearing.

Smell.—For a vicuña to obtain olfactory information of others or their excrement, it is apparently necessary for it to nearly touch the object with its muzzle. It would seem that, for the detection of predators or alien vicuñas, it would be advantageous to have a sense of smell that would function at long range. This sense, however, seems to be poor in the vicuña. On occasions, when I was hidden behind a rock wall several vicuñas approached me to a short distance, evidently unaware of my presence although the breeze bore my scent toward them. In some instances, intruding males remained on the territory of a hostile male, hidden from him by high ground, for a considerable period before he saw them and chased them off. And vicuñas were never seen to react to a fox or dog until it was actually in sight. In fact, they sometimes walked toward a poorly seen dog or man until they saw it clearly, and then they fled. For fleet animals that live in open country and which are rarely attacked by terrestrial native carnivores, a highly developed sense of smell might be of much less value than keen sight.

LOCOMOTION

Gaits.—The basic gaits of the vicuña are the diagonal walk and the transverse gallop (Howell 1944: 228, 233). In walking the order of movement of the feet is: left front, right hind, right front, left hind. The feet of one side move forward at almost the same moment, the hindfoot being placed on the ground an instant before the forefoot of the same side is planted. When a grazing vicuña ambles forward slowly

FIG. 14. As vicuñas gallop across a pampa at high speed, their limber necks keep their heads on a steady course. Near Lago Suche, Moquega; 1952. Photograph by O. P. Pearson.

its feet move in this same order, at intervals of several seconds. In a slow walk the feet move through one cycle during a period of 1-2 seconds.

Vicuñas gallop (Fig. 14) in approximately the manner of the swifter antelopes and deer, which also have a light build, slender legs, curved rump, and tucked-in hindquarters (Howell 1944:241). The supple neck enables the head to travel in a smooth path while the shoulders surge up and down. In galloping at moderate speed, about 20 miles per hr, the legs move through two cycles per sec, each cycle moving the animal forward a distance of about 5 yds. A speed of "at least 30 miles per hour was maintained for some time" by vicuñas chased with an automobile at an elevation of 15000 ft (Hall 1937:472).

Howell (1944:65) suggests that the cursorial ability of camels has been developed for moving long distances between food and water, rather than for fleeing from predators. Perhaps of greater evolutionary importance in vicuñas is the speed and agility of adult males in defending their territories efficiently, and the ability of all vicuñas to avoid the attacks of hostile males. Whatever the reason for the evolution of speed in vicuñas, it is now of great value in fleeing from dogs and horsemen.

Jumping and climbing.—Vicuñas can jump fairly well. At Calacala I saw a domesticated adult female, accompanied by a young juvenile, jump to the top of a 4.5-ft high stone wall, then down on the other side. Sr. Paredes told me that a wire fence 1.8 m (5.9 ft) high was needed to hold vicuñas. They easily jump about 7 feet from one stream bank to the other, and they often hurdle 2-ft high rock walls during normal movements.

Vicuñas climb rocky slopes with agility. At Aricoma I saw them ascend steep shale slides, sending plates of rock clattering down slope. Running adult males thread their way among large rocks, and they mount boulders about 3 ft high in order to view pursuers. In one observation, a troop of 19 males walked 20 yds across a rough solid rock ridge of moderate slope, although they could easily have detoured on grass. The padded soles of the feet apparently do not slip on rock surfaces. In fleeing from men, dogs, or other predators, agility in climbing rough slopes may be of greater value to a vicuña than high speed on level ground.

Trails.—On the better grazing sites vicuña trails are generally inconspicuous, but where vegetation is sparse trails are well-defined. On sandy barren ground pathways are about 8 inches wide and worn an inch into the soil. At close range these paths are obscure, but in strong cross lighting they are easily seen from a distance. At Aricoma, vicuña trails slant across the steepest shale slides above the highest grasslands, and some trails lead over high barren passes. Vicuñas also use llama trails, which in grasslands are conspicuous. Commonly these trails are hard-packed, about 12 inches wide, and worn several inches into the soil. A dozen llama trails may run approximately parallel, a few feet apart, with normal grass cover between them.

FEEDING, DRINKING, AND BATHING

FEEDING BEHAVIOR

Aside from resting the principal activity of vicuñas is foraging. The daily schedule of feeding depends upon hunger, food availability, and the number of hours suitable for grazing. The potential grazing hours are longer in summer than in winter, the maximum difference being about one and three-quarter hours at the latitude of Lake Titicaca (16° S). Not only are days long in summer, but forage is then abundant and succulent. Summer, however, is the season of greatest need for food because of the nutritional drain imposed during this period by the bearing of young and by mating activities. Furthermore, at this season grazing time and efficiency are reduced by frequent storms. At any season foraging requires most of the daylight hours.

Feeding of bands.—The band grazes as a unit, but commonly the adult male grazes at short distance, often 50 yds, from his family. The band members, intimately familiar with one another and the territory, show little system in grazing other than that caused by seeking choice food, yet staying with the group. In the early morning feeding is unhurried, frequently interrupted by rest periods and intergroup encounters. Usually vicuñas start to graze at the site where they rested during the night. Better sites may not be reached until an hour later. In late afternoon feeding is steady, seldom interrupted by rest. Vigorous feeding late in the day is necessary to fill the stomach with food sufficient for a night of rest and rumination.

The rate of movement of a grazing band varies with the richness of the forage. In normal feeding on good range a band may stay within a space 50 yds in diameter for an hour or more. One band remained within a rectangular area of 6 acres for a period of 5 hours. Many bands feed almost entirely within territories less than 40 acres in area. On the other hand, on sandy pampas a feeding band may walk several hundred yards during an hour of grazing. One band of 25 members commonly grazed on a large pampa with its members spread over a distance of more than 200 yds.

In the study areas the preferred grazing sites of most family bands were located on the lower portions of their territories, where the ground was relatively flat, damp, and free of rocks. Usually these bands descended to this lower ground in mid or late afternoon. The descent was sometimes made in one movement of 200-500 yds, but at other times gradually, in the course of grazing. When livestock grazed during the day on the lower flats of the territories of bands A and B at Aricoma, the vicuñas descended after the stock departed. At Huaylarco, at about 4:00 p.m. of most afternoons one familiar band crossed the road in order to graze on a certain gentle slope, while another band habitually walked from a certain canyon bottom to a higher terrace.

For grazing in the late afternoon a certain site may be used consistently by a band. Band A at Aricoma grazed the same small area nearly every afternoon for a period of several weeks. Then it started to favor another site, 200 yds away, and 7 weeks later the band made a similar shift. In this example, the changes seemed to be made in order to utilize the greenest pasturage during a period of increasing dryness.

Feeding of Troops.—In feeding, a troop of males characteristically forms a fairly regular line or crescent which moves slowly in one direction, the individuals a few feet apart. Some move forward and stop, then others move ahead. Those that lie down are left behind the feeding group until finally they rise and run to catch up. Often when the grazing troop encounters a rock slide or other barrier each vicuña turns about so that, within half a minute, the group reverses its direction of movement. Seemingly a line is the most efficient grazing formation, for each animal feeds on grass untouched by others and has freedom of sight and movement ahead. Efficiency in grazing is important to members of a troop because they spend much time on unclaimed ground where food is scarce, and because their feeding is often disrupted by the attacks of territorial males.

Male troops return to the better pastures again and again, even though they have been driven from them. In one observation, a troop of 30 males was fleeing from an approaching shepherd when they encountered 2 aggressive males. These drove the 30 uphill into an area of rocks, but an hour later the troop was grazing at its starting point. Unmolested, in good pasture, a troop may be as sedentary as a family band for many hours. One troop of more than 20 males remained within a 40-acre rectangle for an entire day. Over a period of several days, however, a troop may travel miles.

Feeding of individuals.—Although a grazing vicuña stands with its muzzle almost constantly to the ground, the animal is nevertheless watchful. About every half minute it pauses in feeding and looks around for a few seconds. Under the most peaceable conditions a territorial male, the most watchful member of the band, may keep his head down for a period as long as one minute. Other vicuñas sometimes delay more than twice as long before looking up.

Depending upon the vigor of feeding and the abundance of food, a vicuña grazes 5-30 seconds at one spot before taking a step. Thus, it ambles forward very slowly as it feeds. On sandy grassless pampas each feeding vicuña ambles on a sinuous course, its muzzle constantly near the ground. After each few steps the animal takes a few nips at a plant rosette, its lips making a small depression in the sand. When a vicuña feeds on grassland its jaws nibble rapidly, about five bites per second, and every few seconds it tosses its head slightly as if to tear loose a bite of grass.

In loose soil where vegetation is scant a vicuña sometimes scratches the ground with one forefoot to bare the basal leaves and upper roots of a plant before eating it. One set of scratchings was 4 in deep, 5 in wide, and 2 ft long. Although I have seen prong-

horn antelope paw snow away from underlying plants in order to feed on them, I did not observe vicuñas pawing snow. In snow they fed at uncovered spots, some no larger than their muzzles, or they poked their noses down through the soft shallow snow.

A vicuña may stand in a stream while feeding on bank vegetation (Fig. 4). Frequently it may hold its jaws sideways in reaching under an overhanging bank, the edge of a boulder, or the crown of a tuft of coarse grass. Evidently the spiny tips of coarse grasses are as difficult to penetrate for the vicuña muzzle as for the human hand.

As a vicuña chews cud the tip of its lower jaw describes a symmetrical horizontal figure-eight from side to side. That is, the jaw passes laterally and downward an equal distance on each side of the midline of the muzzle. This chewing motion is in contrast to the unilateral elliptical movement of the jaw of a ruminating deer or cow. The vicuña retains each cud in the mouth about a quarter of a minute, from 25 to 35 chews. The bolus then descends the esophagus and another immediately rises to the mouth, an interval of about 5 seconds elapsing from the cessation of chewing one cud to the start of chewing the next. Vicuñas ruminate while resting, but at slight alarm chewing stops, the cud bulging the cheeks.

Presumably the chisel-shaped persistently-growing lower incisors of the vicuña are of advantage in feeding. Long sharp-tipped incisors of constant length would appear to be highly useful for nibbling very short herbage, as vicuñas often do. In addition, roots and low plants probably contain soil particles that abrade the incisors. Perhaps it is only for certain kinds of feeding that these rodent-like teeth are specialized, for, at least in grass pastures, llamas and sheep seem to eat forage as short as that grazed by vicuñas.

Drinking

The ability of camels to go for long periods without drinking is probably shared, in lesser degree, by most lamoids. Among these the order of increasing water requirements is apparently: guanaco, llama, vicuña, and alpaca. Although vicuñas live in some arid regions, I discovered none at a distance of more than a mile from water. All the vicuña territories studied included water, though in some cases only puddles. In regions of sandy deserts and arid grasslands it is easily seen that vicuñas concentrate in the vicinity of streams and bottoms. The site of drinking may be a rivulet or puddle on a *Distichia* mat, among clumps of grass, or alongside a road, or it may be a pool in a drying streambed, the edge of a lake, or the margin of a swift stream.

Frequency of drinking.—At localities where vicuñas were watched for long periods, they were seen to drink every day, even when the sky was overcast and green food was plentiful. On rare occasions on dry days, a single animal was observed to drink twice, a period of 1-4.5 hours intervening. Drinking occurred as early as 8:00 a.m. and as late as 4:15 p.m., but it did not strongly tend to occur at any certain time of day. Small juveniles were not seen to drink; perhaps milk satisfies their water requirement.

When vicuñas encounter water in the course of foraging, they may drink. In one observation, a band spent the night on a dry slope and in the morning rose and grazed, gradually moving toward an area of green grass and wet mats. Upon first reaching a rivulet the vicuñas drank. In another observation, a band was grazing on a dry slope when a group of alpacas approached. The vicuñas retreated uphill, and when they came to water they drank. At times, when a territorial male is leaving or returning to his females he stops, or deviates from a direct course, in order to drink. Members of a troop may stop and drink whenever the group crosses a stream, even when the troop is under attack.

Manner of drinking.—When drinking a vicuña is wary, looking about before putting its lips to the water. It holds the lips in the water 5-15 seconds, then raises its head to look. As many as 5 draughts are taken, with pauses between. In drinking from a swift stream a vicuña usually puts its lips in calm water near the bank, as if to avoid currents and waves which might drive water into its nostrils.

Drinking by one band appeared to stimulate the same action in a group near by, on occasions. In one instance, a large band drank at the edge of a lake and, a few minutes later, another group drank 100 yds distant. Another time two bands drank, one a few minutes after the other, from the same stream at points 50 yds apart. It seemed more than coincidence that separate groups would simultaneously perform an act that normally occurs but once a day. In many observations, most or all of the members of a band drank within a period of a few minutes. Probably this circumstance was due not only to simultaneous response to water, but to contagion of the action of drinking. As in other actions, it is the adult male that is most likely to be aberrant and drink at a different time than the other members of a band.

Wading and Bathing

Although camels are generally thought of as dry land animals, guanacos are said to swim narrow ocean straits and vicuñas do not hesitate to wade across icy streams. Even tiny juveniles wade. Moreover, while feeding at streambank grass vicuñas commonly stand in water which may reach their chests, and often they bathe in clear streams. The streams where vicuñas were seen to bathe were less than 1 ft deep and from one to several yds wide. Where vicuñas live far from streams they may not bathe for weeks at a time, but some bands near streams at Huaylarco were observed to bathe on two days in succession. No band, however, was seen to bathe more than once a day. Bathing usually occurred in the forenoon, between 10 o'clock and noon.

The bath of a vicuña proceeds about as follows: The bather stands in the stream and slowly lowers its bowed neck until the throat enters the water. Then the animal lies prone in the stream. At this point the hindlegs may be alternately flexed and extended

so that the body souses up and down in the water a few times. Typically a vicuña lies in the water but a few seconds, but on occasions it remains down for a quarter minute. While prone in the stream the bather usually dips its neck until it is wet to the chin. This dipping may be repeated and the neck swished back and forth in the water several times. Then quickly the bather stands, and soon it shakes its body and head. I saw one vicuña repeat the entire bath six times.

As if through contagion of the action of bathing, several vicuñas may bathe at once. Nearly all members of a troop of 14 males bathed within one period of several minutes, many being in the water together. In the water as elsewhere, individuals spit or kick at others that approach them closely. The youngest juvenile seen to bathe was about 2 weeks old; it lay prone in the water a moment, then ran to dry ground. After a bath vicuñas resume grazing in the usual manner.

For the most part baths do not serve to relieve overheating, for they are often taken in cold weather. However, on one warm day I saw 2 females bathe as if to cool themselves. They lay in the water for exceptionally long periods, from one-half to three-quarters of a minute, and, as they proved to be heavily pregnant, they probably benefited from the cooling effect. Inasmuch as flies and ectoparasites were rare in the study areas, bathing seemed to be unnecessary for relief from these pests. Evidently baths are principally of value for cleaning the fleece and maintaining its efficiency as insulation.

PREGNANCY, BIRTH, AND INFANCY

Pregnancy.—By observation from a distance it is difficult to recognize even advanced pregnancy in vicuñas. At Huaylarco I could not distinguish pregnant from non-pregnant females until January, a month before the first birth. But all adult females in the bands appeared to be pregnant in early February. Late in pregnancy the posterior sternal region of the female sags and her abdomen bulges slightly, so that the ventral silhouette of the chest curves into the abdomen without the normal angular contour at the tip of the sternum. Pregnant females are shown in Figs. 4 and 15. On occasions during the last 2 weeks before giving birth, a pregnant female holds her tail a few inches out from her rump for long periods. During these periods the smooth black skin around the anus protrudes about 3 inches. The bulge remains for a period of several seconds, or for as long as 10 minutes, before collapsing. In lying prone heavily pregnant females sometimes place their knees farther back and to the sides than other vicuñas, and in rising they are clumsy. Heavy females usually lag behind the others when a band retreats from danger.

Romero (1927:140) and some later authors give the gestation period of the vicuña as 10 months, but they do not cite the basis for this figure. Sr. Paredes believes the period to be about 11 months, the same as that of the llama and alpaca. Inasmuch as the interval between the birth of the first young at Huaylarco and the first copulation that I witnessed (hardly the first that occurred) was only 18 days, it is probable that pregnancy lasts about 11 months rather than 10.

FIG. 15. Vicuñas run easily over rocky ground. The animal on the right appears to be a pregnant female. Huaylarco, Arequipa; February 27, 1952.

Birth.—In the bands studied at Huaylarco in 1952 the first juvenile was born on February 11. Approximately 25% of the young were born in February, and 45% in the first half of March. The time of appearance of young in each band is shown in Table 1. At the end of April, when observations ceased, less than 10% of the reproductive females still appeared to be pregnant.

Erik Neilsen, who lives near Chuquicamata, Chile, 6° S of Huaylarco, notified me that in 1953 the first young vicuñas were born there in the first half of January. Romero (1927:140) gives the season of birth in Argentina as January-March. Probably, then, in my study area in Peru the breeding season (mid-February to mid-April) is about a month later than in the southern parts of the vicuña range.

Once I observed the actions of a female at the time she gave birth. The event occurred at Huaylarco the morning of February 29, 1952. A band was grazing on its accustomed feeding grounds on a moderate slope. As one female held her tail up most of the time I watched her, suspecting that she was about to give birth. The sequence of events was as follows:

8:56 She lay down on her side.

9:04 Rose, walked to dung pile, defecated. Walked 5 yards with tail up, lay prone.

9:12 Again rose, stood on dung pile as if voiding, but no pellets fell. (Emerging fetus stimulates defecation behavior?)

9:15 Walked slowly 10 yards upslope, scratched ground with forefoot, lay prone 80 yards from rest of band.

9:20 Lay down on side. Abdomen contracted several times at rate 3 per second every few seconds. During strain neck pulled dorsally and upper foreleg raised.

9:22 Rose, nosed ground. Tail highly arched, region of anus and vulva protruding.

9:25 Still standing, tail up. Muzzle fetus 2 inches out vulva. Soon head, ears, one forefoot out. Mother grazed, walking slowly.
9:31 She lay prone, rose half minute later.
9:35 Head fetus hung to level heels mother, forefoot nearly to ground. Then fetus out to waist, quickly slid to ground.
9:36-9:41 As many as nine condors on ground near by. They flew. Mother lay prone.
9:46-10:06 Up to 14 condors on ground. Mother grazed when they 20 yds distant.
10:15 Mother lay prone 5 min.
10:32 Afterbirth dropped.
10:35 Mother walked 100 yds, drank. She remained prone most of next hour.

Afterbirth.—About an hour after parturition the fetal membranes drop from the mother. She holds her tail up, the vulvar region bulges, and the blue-gray amniotic sac, partly filled with liquid, slowly emerges and hangs down behind her heels. Soon the placenta breaks loose and the membranes drop. One afterbirth, emptied of 5 lbs of cider-brown odorless fluid, weighed 1.5 lbs. The diffuse placenta, a bag with a rough raw outer surface where the chorionic sac broke away from the uterine wall, was 16 inches long.

In my 4 observations of the dropping of the membranes, they fell to the ground 1-8 minutes after starting to protrude. The only reaction of the mother to the fallen afterbirth was to hold her nose close to it for a few seconds. In some kinds of ungulates the mothers eat the afterbirth, but evidently vicuña mothers do not. Nor did other vicuñas or raptorial birds show interest in afterbirths which lay on the ground.

Activity of the infant.—The first actions of the infant at the time of the birth described were as follows:

9:26 Head and foreleg out vulva. Shook head rapidly, ears flopping.
9:33 Entire neck hung out, limply. Occasionally shook head.
9:36 Fell to ground; thrashed legs; lay prone.
9:47 First tried to rise; onto knees; fell.
9:49 Rose onto wrists, hindlegs. First stood; legs widespread, wobbly; fell.
9:58 Again stood; fell. Could raise tail vertically.
10:01 Stood 1 minute; fell; lay prone. Stood; head first under belly mother; fell. Stood 2¼ minutes; nosed belly mother; fell.
10:07 Stood 4½ minutes; fell. Rose; staggered 50 feet beside mother.
10:15 Lay on side 1 minute. Stood 4½ minutes; shook head; walked; short staggering run.
10:20 Gamboled, taking two small jumps per second in running. On feet more than 12 minutes.
10:35 Followed mother walking 100 yards up across rocky moderate slope.
10:38 First nursed (1 hour old). Prone most next hour.
11:50 Wool dry. Wobbly when ran. Feet raised high in walking.
12:20 Ran more than 200 yards across rocky slope with mother. Estimated speed 15 miles per hour.

Twenty minutes after birth an infant vicuña can hold its neck and head up but it cannot stand (Fig. 10). Three-quarters of an hour after birth it can run a short distance. At that time its coat is fairly dry, but scraggly and rough. Mucus that coats the back of the newborn dries into an irregular membrane which may persist for a day. As judged by the actions of five newborn vicuñas, during the first day of life the infant walks and stands very unsteadily, hindlegs spread wide. Occasionally it runs a distance of about 10 yds, but most of the first day the infant remains lying down. It rarely stays down for a period of more than 15 minutes, but on the other hand it seldom stays on its feet for longer than half an hour. When lying down the newborn often rests its head sideways on the ground, eyes nearly closed, and dozes. If the infant dozes while lying prone with head up, the drowsy head may gradually drop forward until the muzzle touches the ground. Then quickly the youngster raises its head, but soon it nods again. Again, its head may nod backward, dropping slowly until the muzzle is vertical and the ears touch the back before it is lifted again.

Infants 1-5 days old are rarely seen more than 30 yds from an adult vicuña. In play the youngster may run 10-20 yds from the band and back again, or jump straight up into the air. It is easily disturbed when resting, often remaining down for a period of only a minute or two and seldom for longer than 20 minutes. While resting infants doze a great deal, frequently with the muzzle tilted up about 20°. And on rare occasions they bite at the ground and then chew a bit, as if eating grass.

From 6-10 days of age the tiny juvenile gambols playfully, rearing up on its hind legs, turning sharply this way and that, dashing among the adults, and running as far as 50 yds from the group and back again. Like older juveniles, infants are most frolicsome in the late afternoon. At 10 days of age the youngster still lies down and rises frequently, but it may stay down for an hour, and it usually dozes while resting. At this age also, young graze in a dilatory manner and chew cud.

FAMILY BANDS

Composition and Size

Average composition.—A century ago Tschudi (1847:312) stated that vicuñas live in bands "consisting of from five to fifteen females, and one male. . . ." This statement is substantially correct for family groups if juveniles are not included. At Huaylarco in December, before many yearlings had left the bands and before the new young were born, the average band consisted of 8 members: an adult male accompanied by a family of 7, 2 of these being old juveniles which would become yearlings in January (Table 1,

totals). The 15 bands censused in December had 2-15 members, including as many as 5 old juveniles. The largest band without any juveniles contained 9 members.

While motoring through unfamiliar regions during autumn, winter, or early spring, one can recognize many groups of vicuñas as family bands because they include young juveniles. In 30 bands that I censused at various sites in Peru between April and September, and which contained juveniles, the average family accompanying a male consisted of 1 juvenile and 3 or 4 older females (including yearlings). In 14 bands with juveniles that I saw between Ocoruro and Pati one day in October, 1951, the average family was 1.3 juveniles (1-3) and 4.1 older females (2-8). At Huaylarco, where the population density was high, the comparable (early November) average for nine bands having young was 2.9 juveniles and 5 older females per family. The average number of juveniles and females would have been less if families without small young had been included in these counts, but it was difficult to distinguish these groups from small troops of males.

Minor changes in composition.—A band of vicuñas is a closed society from which established members do not readily withdraw. The size of a band may change little over a period of months. Some bands remain large. Band S. 139.0 had 7-11 adults for 5 months (Table 1, December to April). Band E. 139.0 had 6-8 adults for 6 months (November to April). Band S. 133.0 had 9-13 adults for 4 months (November to February). Other bands remain small. Band E. 138.8 had no more than 2 adults for a period of 4 months (January to April). At Aricoma, a single adult male occupied one territory for at least 4 months (June to September).

A more detailed summary of the changes in composition that occurred in two bands studied at Aricoma is given in Table 3. These bands, A and B, were of about the same size and they occupied similar adjacent territories. However, the composition of band B fluctuated much more than that of band A. In approximately equal periods of watching (62 and 65 days), only 7 changes occurred in the composition of band A but 12 changes were detected in B. The reasons for this difference were, in part, the greater belligerence of the male of B, and the fact that his band was close to the normal line of movement of other vicuñas and of livestock and thus was subject to frequent disturbance.

Most changes in the composition of bands are the result of the joining or departure of 1 or 2 females or young. As late as November, when juveniles are about 7 months old, mother and juvenile usually join or leave a band together. For example (Table 3), band B gained a female and juvenile on July 16 and lost them on the evening of July 18. Frequently one or two females join a band and remain for only a day, or for part of a day. The individual last to join a band is often the next one to leave it, even

TABLE 3. Summary of observed changes in composition of two bands. Aricoma, June to October, 1951.

Band	Period of Time	Number in Band	Composition[a]	Net Change[b]		Number of Days Observed
				Gain	Loss	
A	June 11 - 25	5	M 4 females			9
	July 4 - 28 (5 p.m.)	5	M F fff			16
	July 28 (5 p.m.) - Aug. 15	6	M FF fff	F		12
	Interruption					
	Aug. 27 - Sept. 1	3	M F f		F ff	4
	Sept. 3 (a.m.)	4	M F ff	f		1
	Sept. 3 (p.m.) - Sept. 24	3	M F f		f	15
	Sept. 26 - 28	4	M F ff	f		3
	Oct. 1 - 3	3	M 2 females		F or f	2
B	June 2 - July 6	3	M F f			16
	July 10 - 15	4	M FF f	F		4
	July 16 - 18 (p.m.)	6	M FFF f j	F j		2
	July 18 (p.m.) - July 19 (p.m.)	5	M FF ff	f	F j	1
	July 20 (all day)	7	M FFFF ff	FF		1
	July 21 - 30 (a.m.)	5	M FFF f		F f	7
	July 30 (p.m.) - Aug. 15	4	M FF f		F	11
	Interruption					
	Aug. 30 - Sept. 3	4	M FF f			5
	Sept. 4	3	M F f		F	1
	Sept. 5 - 7	4	M FF f	F		3
	Sept. 8 - 11	3	M F f		F	2
	Sept. 12 - Oct. 15	4	M FF f	F		12

[a] M = adult male, F = one adult female, f = one immature female, j = one juvenile.
[b] Absences of a member for fraction of a day are not included.

though this animal remains with the group for several days. This fact suggests that some females are more strongly attached to the territory, male, or group than are some others. If all females changed bands with equal freedom, a band with twice as many females as another would have twice as frequent changes in composition. No such direct relation was noted. Nevertheless, single territorial males tend to remain alone, and exceptionally large bands, of 15 or more members, change composition rather frequently. Minor changes in numbers seem to be caused principally by the movements of a small number of females that are not strongly attached to one band or territory.

Major changes in composition.—In the event that a territorial male becomes sick or injured, his family soon disperses. This event occurred in 3 bands under study at Huaylarco. The first example involved band W. 138.2, which consisted of 4 adults and 2 yearlings for several weeks prior to January 12. On that day the yearlings were gone. The 4 adults remained in the band until January 17. The next day the male was alone on his territory. He was very weak and was barely able to stand. That his territory was undefended was evident from the fact that a large male troop grazed close to him, unmolested. During the next 4 days the sick male recovered. On January 24 he seemed to be in good health and he defended the territory, but on one side he defended only to a line about 200 yds short of the former boundary. On January 28, 10 days after the loss of his females, and for at least the following 3 days, this male was accompanied by one yearling female. Several days later the male had a family of 3 yearlings. This band of 4 members remained unchanged until the end of April.

The second example concerned band S. 133.0, which had 13 members, including a young juvenile, during the last two weeks of February. On March 5 a group of 4 females with 4 juveniles, unaccompanied by a male, was seen on the territory, and another group of 4 females was seen half a mile distant on a neighboring territory, N. 134.5. Two days later the favorite grazing site of band S. 133.0 was occupied only by a large troop of males. I saw some females and juveniles join band N. 134.5. This band increased by 9 adult females between March 5 and 7. Another band in the vicinity (S. 135.6) increased by 2 adult females in the same period. Thus, the 11 adult females lost by band S. 133.0 had apparently separated, 9 and 2, and joined two separate bands. On March 10 an adult male, presumably the male of the former band S. 133.0, was seen on that territory. He was alone and lame, and a neighboring band (N. 133.0) grazed unmolested on the former preferred grazing site of band S. 133.0.

The third example involved band W. 139.4. This consisted of 9 members, including 2 juveniles, for several days before March 20. On March 21 only the male, a distinctively marked individual, was present. He was sick; one eye was swollen closed. His entire family, including the juveniles, was in the band of a neighboring male, also distinctively marked. During the previous several weeks the latter male (W. 139.0) had had only 1 or 2 females. Now he had 8 females and 2 juveniles, and this band remained approximately the same for the next month or longer. The injured male was later seen at sites away from his territory, but two weeks after the band broke up he was back on his territory with an adult female. These two remained together for at least three weeks.

Maximum band size.—At Huaylarco the maximum numbers of members in single bands, not counting young juveniles, were 18 (band S. 133.0 in January), 17 (S. 133.2, March), and 16 (E.137.5, November; N. 134.5, March). Including young juveniles in the count, the largest numbers noted were 26, of which 9 were juveniles (S. 133.2, March), and 23, of which 8 were juveniles (N. 134.5, April). In January, before new juveniles were born, 30% of the bands had at least 10 members. The number of members in the largest bands was greater in areas of high population density, such as Huaylarco, than in areas of moderate or low population densities. At Aricoma, where many counts were made between June and September, the largest 2 bands observed had totals of 12 and 10 members, each including 2 juveniles. Of 30 other bands seen at various localities in Peru during the period from April to September, 1951, the 2 largest had 17 members, including from 2 to 6 juveniles.

The limit of family size, a maximum of about 16 reproductive females, might be the result of the inability of the male to protect more with efficiency. Is there, then, a direct relation between the pugnacity of territorial males and the size of their families? It is difficult to detect evidence for such a relationship because the females seem to be kept in their territory more by the belligerence of neighboring males than by the action of the male of their own band. Even though a male is capable of protecting his territory, much time may elapse before an unattached female happens to enter it.

The relative pugnacity of neighboring males is, however, often a factor determining the size of bands. As shown earlier, sick males lose their families. At Huaylarco, relatively docile males (N. 133.5, W. 138.6, and W. 138.2 after January) sometimes had a few yearlings but rarely an adult female in their bands. Apparently weak males cannot well retain adult females. On the other hand, one vigorous male (W. 139.0) had only 1 or 2 females for more than 3 months before he gained 7 more through the illness of a neighboring male. A lone male at Aricoma defended his territory aggressively; yet, in a period of 4 months he acquired no females. It seems that the size of a band at a particular time depends largely upon the occurrence of opportunities for increase.

Yearlings in bands.—At the time that young are born yearlings are rare in family bands. Of the 20 bands studied at Huaylarco, infants were noted in 12, but only one of these bands contained a yearling at the same time. However, during the same period (February to April) of 8 bands without juveniles all (save one lone male) had at least one yearling. Commencing in December there was a steady loss of

yearlings from bands (Table 1, totals). In late November there were 48 near-yearlings (old juveniles) per 100 older females. By March the ratio had dropped to 13, a loss of about 75% of the yearlings. In bands having new juveniles the loss of yearlings was 100%. Assuming a balanced sex ratio in young, it appears that usually both sexes of yearlings leave the bands, especially those bands having new young. If all yearlings left bands having new young, and if only the male yearlings left the bands not having new young, the loss of yearlings from bands would be about as observed at Huaylarco.

Perhaps the situation in vicuñas is similar to that in roe deer. "The does drive away their young ones when they are yearlings if new calves are born then, and the bucks will not tolerate the presence of another male in the group beyond the age of a yearling" (Darling 1937:93). In vicuñas, though, yearlings were not seen to be driven out by adults of either sex. The statement of Tschudi that the band females drive out the yearling males with bites and kicks is often repeated in the literature, but it is not corroborated.

In early November juvenile males were first seen in male troops, but as late as February some yearling males were still members of bands. For a few weeks before February 22 one band had two yearlings, a male and a female, as well as several adult females. On February 24 the male yearling was gone, but the female disappeared only a week later. Perhaps both sexes of yearlings leave the bands at about the same time. Probably yearlings leave the family simply because their mothers cease lactating, or, if new young are born, because the mothers refuse to nurse the larger young.

Soon after leaving their mothers the male yearlings join troops. But what becomes of the yearling females? Most of them probably join other bands or solitary territorial males. Three yearling females joined one adult male after the dissolution of his family Table 1, W. 138.2, February). Another male lost his entire family of 13 but soon acquired 2 yearling females (E. 137.5, February). A lone male (N. 133.5) had 1 or 2 yearling females for about a week in February, but none for several weeks before and after. In late January 2 bands without yearlings (E. 138.2, W. 139.4) each gained one. A yearling joined the 2 members of another band (E. 138.8) in April. Possibly a few yearling females remain in those bands that have no new juveniles.

Assuming a 1:1 sex ratio in yearlings, only about half of the yearling females lost from bands in the study area were accounted for by additions to other bands. This uncompensated loss of yearlings accounts, in part, for the low average size of bands in February (6 members including one yearling) as opposed to December (8 members including 2 near-yearlings). A few yearling females could have wandered about and been mistaken for scattered troop males. Possibly some became temporary members of troops; I would not expect immature males to be very hostile toward them. But many probably joined bands outside of the study area. That an equal number did not move in and balance this loss might be accounted for by the fact that the population density in the study area was high as compared to the surrounding region, and the dispersal of yearlings may have been principally outward toward less populated areas.

The strong probability that the forcing out of young from the families of territorial mammals is important in determining the rate of dispersal of species has been pointed out by Burt (1949:26). The departure of yearlings from vicuña bands is one means of dispersal. After leaving their families, yearlings probably move about considerably. Yearling males are prevented by family males from joining bands. Yearling females, too, meet antagonism from bands, especially from the female members, and so they might often join males that hold marginal territories.

NON-SEXUAL RELATIONS BETWEEN MALE AND FEMALE

Concern of the male for his females.—The male is the protector and leader of the family. Normally he grazes close to it. When other males approach, he runs to challenge the intruders at the territorial boundary. This sally, as of the besieged against besiegers, I have called a "sortie." After a sortie the male returns to a point near his family. While he is away, he often stares back toward his females, as if to make sure that they are not being attacked. If the females are approached by another male, the resident male quickly runs back to them. In a typical sortie the male stays away for less than 10 minutes, but the interval may be much longer. One morning the male of a large band ran a few hundred yds from his family at 8:10 a.m. in order to chase a large troop of males. Twenty minutes later a neighboring male moved to a point approximately 100 yds from the unguarded family, but he remained on his own territory. Not until half an hour after he departed did the resident male return and graze 100 yds from his females. And yet another half hour elapsed before he reached a point less than 50 yds from them.

A female that rejoins the family after an absence of several hours elicits only mild attention from the male. One evening I noted that two females of a certain band were absent. The next forenoon one of them returned. As she approached the band, the male walked toward her. She stood fast and the male halted nearby. Then, followed by the female, the male walked back to the family group and showed no further interest in her. On another occasion, an immature female walked away from a band and over the top of a ridge, 200 yds from the group, at 7:00 a.m. The family male followed for 100 yds, then stopped. Soon dogs drove the vicuñas from their territory, but at 1:30 p.m. they returned, still without the immature. An hour and a half later the wandering one pranced toward the band, tail up, and halted 15 yds distant. Although at first the male walked toward her, she joined the band without further attention from him. Yet again, early one morning I noted that an adult female was missing from one band. An hour and a half later the band

male, tail up, loped 80 yds toward an adult which proved to be the returning female. She ran past him and he pursued for several yds. But she grazed with the other females and he did not molest her.

The mild initial belligerence of the male toward his own returning females is probably due to a delay in his recognition of them. Once as I was watching a male herding a troop of young males in his territory, he suddenly dashed off to the side and up a slope as if to attack a single immature vicuña that stood at a distance. When the male reached a point 50 yds from the immature, the latter raised its tail high. The male stopped, turned, and galloped back to attack the troop again. The single one was his own and only female, which he apparently did not recognize until close to her.

Vicuñas differ from species, such as the fur seal, that vigorously maintain a harem in mating season, in that the male vicuña does not actively prevent females from leaving his band or territory. Nevertheless, one observation suggested that, on rare occasions, a male might make a strong effort to keep established females in his band. Early one morning in July, band A was resting on its territory, but one member, apparently the male, was absent. A few hundred yds distant stood a group of 7 vicuñas, probably a displaced band. One of these, evidently a male, galloped to the females of A, and confused chasing ensued. The attacker drove the 4 members of band A to the larger group. Another melee took place, a few vicuñas ran off, and several remained. These proved to be band A, now including not only its male but 2 additional females. Three-quarters of an hour later a single male approached the band. Although he was chased energetically by the resident male, the stranger reached the cluster of females. Twice he herded 2 females out of the band; each time the family male chased the females back to his group. Once more the stranger started away herding 2 females in front of him. The resident male followed them for 200 yds, then stopped near his territorial boundary. Band A now consisted of 5 members, as on the previous day. My interpretation of the foregoing action is that the resting females of band A were attacked by the male of another band, which drove them to his own family group. The male of band A then returned and attacked this group. The intruding male was driven off, but he left 2 of his females behind with band A. Later the alien male returned alone and, in spite of attacks by the resident male, succeeded in herding off his lost females. It was this last act that appeared to be most unusual.

One observation illustrated the attention of a family male to the actions of one of his females which had evidently lost her newborn young. That morning in April the last pregnant female of band E. 139.0 seemed about to give birth. The band was absent from its territory at midday, but returned at about 4:20 p.m. The only female without a juvenile slowly ran to a point 200 yds south of the band. The male soon ran after her. He stood several yds from the female and looked about; then, followed by the female, he ran back to the band. Soon this action was repeated, the two returning in company. Twenty minutes later the female ran 150 yds south of the group. The male ran halfway to her. Within a few minutes the female returned to a point near the male. Once more she ran south, this time a shorter distance, before returning to the band. The concave sides of this female, her subsequent non-pregnancy, and the fact that a condor landed near the site the following day, suggested that this female had born and lost her young in the vicinity to which she returned again and again. Whatever drove the band from its territory that morning (dogs, condors?) might also have destroyed the infant.

Following and leading.—Tschudi (1847:312) was accurate when he wrote that upon alarm the male of a band gives a whistling signal, the females draw close together, and the band moves off, the male guarding the females from the rear. But on the other hand, when the family group moves from one feeding area to another the male leads. Nearly every afternoon at Aricoma bands A and B descended over the brow of a slope and walked down to a flat area that was favored for grazing. In this movement the groups usually walked a distance of about 300 yds, the males leading. On occasions the male ran down the final slope while the females were still at the brow of the hill, and they descended several minutes later. At Huaylarco too, when certain bands walked to favored grazing areas in the late afternoon, the males preceded the females by a distance of 50-100 yds.

In an action witnessed at Aricoma, a territorial male appeared to herd his family for a distance of three-quarters of a mile up and across a steep rocky slope to an isolated grassy bowl. One morning I saw 6 vicuñas grazing at a site normally used by a band of 7. Evidently the 6 were the females of the resident band, the male being absent. A short time later a belligerent male, vigorously herding several vicuñas before him, passed across the slope a few hundred yds uphill from the resident family. The family started walking uphill. After driving the alien group on for a quarter-mile, the male returned across the slope and followed the family, apparently his own. The band walked fast upslope, the male from 10-100 yds behind the females, and started up a long rock slide. Higher and higher the vicuñas climbed until, more than half an hour after commencing to walk, they stood atop a barren ridge several hundred ft above the level of their starting point. During the entire climb the male acted as if mildly herding or driving his family onward. Then the group descended a short distance to the grassy floor of a cirque that had, on another occasion, been their retreat when alarmed.

In this observation there was no obvious cause for alarm, although nearby horses could have caused a disturbance shortly before my arrival. A few days later I saw this band of 7 at the lower site from which it had started. Not improbably the band used two grazing areas separated by long barren slopes and the observed action was a movement, instigated by

mild disturbance, from the lower area to the upper.

Attraction of females to the male.—While the male is absent from his family for a short period, as during a sortie, the females graze or rest as if unconcerned. But if the male stays away several minutes, or if he returns only part way to the females, they amble toward him as they graze. Before walking toward the male, however, the females may wait for a period of 10-20 minutes, and they often require an equal period to reach him. If the male runs back toward his family after an absence, the females stare intently at him, and they may run a few steps toward him with their tails high. This is the first reaction of any vicuña to the sudden approach of an "unrecognized" animal.

On occasions I saw an adult female follow the male for a distance of about 5 yards as he started off on a sortie. In a few observations, made early in the year (February), I saw one or more yearling females accompany a male on a sortie. One yearling followed the male to a point 100 yds outside of his territory, when he was attacking a troop. In each observation there were no older females in the band. Probably for a few weeks after young are separated from their mothers they tend to follow any adult near at hand.

Alarmed females sometimes appear to seek the protection of the male. In one observation, the family male was on the opposite side of a stream from his large family when an automobile engine was started nearby. At the sound the females ran across the stream toward the male, in the direction of the disturbance, not away from it and toward the hills. It was apparently first related by Tschudi (1847:312), and has often been repeated since, that if the male of a band is wounded or killed the females will gather around him and will not flee. I doubt that this is true, for the male usually runs behind retreating females, and wounded males lose their families within a day or two.

Male dominance.—The dominance of the male over the females of his band is not disputed by them. When he approaches to within a few yards of a female, she quickly walks away, her ears depressed. If a female is lying down when the male nears, she rises quickly, raises her tail, takes a few quick steps, and sometimes spits into the air. Often a group of females sidles away as their male walks toward them.

At any time of the year, not only in the mating season, the females of a band may be chased by the male. In one observation the male voided, ran to his cluster of females, and chased one for a distance of 100 yds before both stopped. They stood 30 yds apart for a moment; then a shorter chase ensued. Brief pursuit of the females by the male is most common at the time when he is challenging another male or returning from an encounter. Such pursuit often serves to drive the females back deeper into their territory, away from the challenged intruder, but it might be caused only by the fact that the male is irritable under these circumstances. In one observation, the resident male ran back to his unguarded females when an alien male started to chase them. The alien quickly fled, but the band male then pursued his own females for 100 yds and gave a hoarse cry. In another observation, the male of a band chased the "winner" of a brief fight between 2 of his females. Occasionally a male chases females that try to join his family or which have joined recently.

Although male vicuñas often attack females in captivity, they rarely do so in the wild. A fight between an adult male and female was seen only twice, both times in February when most females were heavily pregnant. In one fight the male bit the flank of a female and she kicked back at him. In the other encounter a male and female reared up and clashed their forelegs together.

SEXUAL RELATIONS

Season and age of breeding.—The rut follows about one month after the period during which young are born. In contrast to male deer, adult male vicuñas do not undergo changes in appearance and behavior during the breeding season, except that they sometimes pursue females in order to copulate. Copulation by yearling males would rarely be successful in the wild, for if one of them approaches the females of a band he is driven off by the family male. In addition, because of his smaller size a yearling male would seem to be unable to copulate efficiently with an adult female. Furthermore, although domesticated vicuñas are reported to be capable of reproduction at one year of age (Romero 1927:140), wild vicuñas may not be fertile until they are several months older. The testis of a yearling male about 16 months old (July) measured 17 x 13 x 10 mm. It was inactive. But the testis of a two-year old in mid-March measured 25 x 17 mm and was actively producing sperm. Spermatogenesis apparently continues the year round, for all stages were found in the testis (measuring 36 x 25 x 22 mm) of an adult in late September.

Although I saw an adult male copulate with yearling females, I am not certain that any females in the study area gave birth at two years of age. Apparently, the fertility of yearling females is low in the wild. On haciendas alpacas are usually not bred until they are two years old (Maccagno 1932:35). For population analysis of vicuñas, I consider yearlings to be non-breeders.

Copulation.—Lamoids are polygynous. In alpacas, as in ranch vicuñas at Calacala, the customary ratio of reproductive females to males is 10:1. At Huaylarco, on 5 separate occasions between March 1 and April 15, I observed sexual intercourse in vicuñas. Two observations were made on one day, and two involved the same male. Two observations were made before 7:00 a.m., the other 3 about noon or shortly after. In 3 instances an extra female, not present in the band on other occasions, was with the group when coition took place. In two instances, shortly after coition a female, surely the one bred in one instance, walked away from the band and did not return. Perhaps receptive females are attracted to adult males before copulation but, not being estab-

lished members of the band, they tend to wander away afterward. One male copulated with 2 females in succession. The band male probably mates not only with the females of his family but also promiscuously with unattached females.

Mere mounting does not indicate an attempt at copulation. A juvenile may straddle the back of another in play-fighting. In one observation, a pregnant female chased another female for several yards and straddled her. She repeated this act 3 times. In sexual mounting the male straddles the small of the back of the standing female with his forelegs. Usually she lies prone and submits to him within several seconds, though she may remain standing under his weight for a minute. Once when the mounted female did not accommodate the male by lying down, he worked his chest forward on her back and brought his full weight to bear on her by raising his feet off the ground. After staggering a few seconds, the female quickly turned sideways beneath the male so that his chest and forelegs were at right angles across her back. Soon the male dismounted and ran off.

In coitus the female lies prone as in resting. The male lies prone upon her back, straddling her chest with his forelegs, his head above and slightly to the rear of hers. His forelegs rest on her back, his flexed wrists or elbows press close behind her scapulae, and his forefeet are clear of the ground. The strongly flexed hindlegs of the male are placed lateral to those of the female, his metatarsi resting flat on the ground, the thighs of the two being nearly parallel. The male holds his sacral region vertically close behind the rump of the female, the base of his tail about four inches above the ground.

As copulation proceeds the female lies quietly, her ears back. From time to time she turns her head and neck with normal alertness. She may lift her head and nuzzle the chest or chin of the male, or spit at his head. In one observation, after several minutes of intercourse the female rolled onto her side, causing the male to rise, but soon copulation resumed. This interruption was repeated twice more in the same manner, at intervals of several minutes.

In contrast to the calm of the female, the male is excited during coition. His ears tremble constantly, his nostrils dilate and flatten at short irregular intervals, and his tail flips up and down. At intervals he squirms and wriggles as if to get as far forward as possible on the back of the female. One male pushed his closed mouth against one ear of the female, and for several seconds held it pressed flat against her head. He did this several times. Pelvic thrusts an inch or two in length are usually given at an irregular rate, from one to three per second, but occasionally the pelvis of the copulating male remains motionless for an interval of a minute or longer. One intercourse terminated with a dozen very slow strong thrusts.

Usually the copulating male pays little attention to the activities of nearby vicuñas. In one observation, however, he quickly got up and, followed by his mating partner, dashed after three yearling females. Soon he resumed copulation with the same female, but again he rose and ran after the yearlings. One of these, her rump toward the male, switched her tail rapidly from side to side. The male copulated with her. The next time that the yearlings approached close to him, he blew at them. In another observation, a copulating male gave only a toss of his head when a small juvenile nosed his side.

In general, family members standing close at hand take little notice of the copulating pair. In an exceptional instance, 3 yearling females, necks and heads outstretched, slowly walked up to the male, and then walked away. They repeated this action while the male copulated with a second female. In another example, a tiny juvenile nosed its mother, with which the male was copulating, and nuzzled the side of the male. Then another female and her infant nuzzled the male. But after the first 5 minutes of copulation, the many females and young of the family showed no interest.

After completing an uninterrupted coition with a cooperative female the male pays no particular attention to his sexual partner, or to other females, but if copulation is broken off the male takes action to resume it. After one intercourse was interrupted for the third time by the rolling over of the female, the male chased her a distance of 50 yds. In another observation, a male broke off copulation to chase three females. He kicked back at one that passed close by, then mounted another and copulated. Following a second interruption, he chased his partner and straddled her back, but before she submitted to him he dashed away to chase another male.

My most complete observation of copulation and associated activity was of band N. 134.5 which consisted of 23 members, including 8 juveniles, on April 15, 1952. At 11:50 a.m. the male stood 30 yds from the group of females. Suddenly he ran into the group, head and muzzle high as if spitting, and chased a mother. Three times the pair ran back and forth a distance of about 30 yds before the female stopped. The male mounted her, she lay prone a minute later, and copulation commenced. Thirteen minutes later the female stood up. But as the male remained astride her hindquarters, she was able to stagger only 20 yds with her burden before again lying prone. After copulating for 7 minutes more, the male stood up and grazed. When the female arose her juvenile immediately commenced to nurse. During the next hour this female grazed close to the male, but neither seemed to notice the other, and there was no further sexual activity in the group.

Male chasing female.—On 5 occasions (February 18-April 10) I saw a male chase a female, or persistently follow her, in a manner suggesting that copulation was imminent. While pursuing the female the male sometimes gave long squeals or guttural cries, or he spit at her. Eventually she stood still and the male cautiously held his muzzle close to her anal region. In response to this, one female kicked back at the male, but usually she raised her tail high and

thrashed it rapidly from side to side. In one observation, a male vicuña copulated with a female immediately after she waggled her raised tail. Sometimes the male repeated the "interested" actions after many minutes of normal activity, or he alternated his attentions between two females. In 3 of the 5 observations the active male and female were not on their territories. This fact suggests that on occasions the male may chase a female to a point outside of his territory.

In one observation a male interposed himself between a female and a group she was trying to join, preventing her from joining it. When finally she ran away from the group, the male followed, tail high. Then for a period of half an hour he walked close behind or beside her, and occasionally he chased her. From time to time a territorial male chased this pair. On these occasions the male member of the pair kept between the attacker and the female. And when she attempted to join other bands her partner interposed himself between her and the group. Most of the time the female held her tail slightly arched, and frequently she thrashed it from side to side and looked back over her shoulder at the male. The two traveled about a quarter mile from the starting point, but eventually they returned to it, and soon they walked off in another direction.

On another occasion, I saw what appeared to be the return of a male and female to their territory after a long pursuit and probable copulation. Early one morning the two walked toward the territory from a point a few hundred yds distant. The matted wool of the shoulders of the female indicated that the male had straddled her recently. Ten yds behind the female walked the male—lips agape, wool damp, and blood on his neck. Once he dashed 30 yds toward another male which approached, and later he ran at a yearling. The pair walked into the territory and grazed. Evidently the male was the holder of that territory, for the next day I noted that the resident male there had a fresh cut on his neck at the spot where I had seen blood.

In June at Aricoma, after breeding activity had subsided, I sometimes saw a male showing apparent sexual interest in a female. In one observation, a female ran out of a band to a point 30 yds distant and halted. The male ran after her and cautiously nosed the region of her raised tail. At this, she kicked, ran forward several steps, and halted. The male nosed her and she retreated 6 more times. But soon thereafter the entire band grazed peacefully.

Reaction to odor of excrement.—A mannerism characteristic of male vicuñas is the action of tilting the head up vertically, muzzle pointing toward the sky, immediately after nosing a dung pile. I call this action "sky-pointing." When the head is highest the neck curves upward about 90°, the ventral outline of the jaw is approximately vertical, the ears are far back, and the incisors are bared. As the male raises his head he may shake it rapidly, as if ammonia had penetrated his nostrils. Presumably the whole act is caused by the odor of urine. Often a male sky-points just before or just after he voids.

An action similar to sky-pointing is performed by stag red deer (Darling 1939:175, 176) and some other ungulates during the rut, but in vicuñas this action by adult males was not found to be more common in the mating season (March-May) than at other times of the year. Nevertheless, outside of the mating period sky-pointing is often an apparent response to the voiding of a female. In one observation in August an adult male, then an immature female, voided on the same dung pile. The male then approached the female from the rear and she walked away. Then the male nosed the dung pile and sky-pointed. In an observation in November, a male quickly walked to a dung pile where a female was defecating, nosed the pile, and sky-pointed. He repeated the last two actions seven times in succession.

Sometimes a male noses the excrement of a female, sky-points, and then chases the female. Here are some examples. In January an adult male challenged a male troop, nosed a dung pile, sky-pointed, and then chased his own females a distance of 50 yds. Again, in March, just after a female voided, the family male nosed the dung, sky-pointed, urinated, ran after one new mother, and chased another female for a short distance. One day in July, a band male walked 30 yds to a dung pile just used by a female, nosed the feces, and then chased the female a short distance. Soon two other females used the same pile. The male returned to the dung, nosed it, and ran a few steps toward these females.

Immature males as young as 8 months of age were seen to sky-point. One yearling performed this act after nosing the raised tail of another male, which was urinating at the time. Frequently troop males sky-point after nosing the fresh excrement of their fellows. Observation of this action frequently aided me in distinguishing male troops from family bands.

Normally female vicuñas do not sky-point, but on a few occasions during the season of birth and mating I saw females perform this act. In one observation (February), two pregnant females sky-pointed just before defecating. One of them repeated the act a dozen times (more times than observed for any male), nosing the dung pile for several seconds, then lifting her muzzle high, shaking her head as she raised it. Probably a hormonal condition or increased sensitivity to odors that occurs during the breeding season causes females to sky-point then. On occasions at any time of the year, a female may shake her head after nosing the tail region of another.

RELATIONS BETWEEN MOTHER AND YOUNG

Nursing.—When the infant is only a few days old, its mother may initiate nursing by nosing the resting juvenile, causing it to rise; then it sucks. Normally, however, it is the juvenile that initiates nursing. At first the youngster nuzzles the head or side of its mother, then it noses her belly. At this the mother may rebuff the juvenile by bringing her knee forward and up against its head or neck, by walking away from it, or by pushing its head aside with hers. She

may even kick at her young one. In spite of rebuffs, an infant a few days old usually makes repeated attempts to suck, and, if repulsed at one side of the adult, it tries the other. Older juveniles, apparently conditioned to refusal, usually do not try to suck if the first attempt fails.

The young vicuña nurses calmly, in the approximate manner of the calf of a milk cow, usually standing with its body alongside the chest of its mother. As soon as the juvenile commences to nurse, its mother puts her nose to its flank or tail region as if to verify by smell that the youngster is hers. Then she stands quietly, ears back, hindlegs slightly spread, and continues to chew cud. Sometimes the mother grazes and, as she walks, the youngster sidles along to keep up. Frequently a juvenile commences to nurse while its mother stands spread-legged at a dung pile, as if the defecation posture invited nursing. Perhaps too the sight of other nursing young stimulates the act, for often I saw two young of a band being fed at the same time.

The period of nursing is usually ended by the mother. She turns sideways toward the young one, causing its head to be withdrawn from her belly, or she walks forward, pushing away the head of the suckling young with her knee. In some observations the youngster then followed its mother and attempted to nurse again. One infant, two-days old, walked close behind its mother for three minutes and several times thrust its head between her thighs. Sometimes the mother permits an infant to resume sucking for a period of about a quarter of a minute.

An infant but a few days old usually lies down within an interval of one minute after nursing. Young from one to several weeks old normally lie down within 10 minutes after taking milk, and this tendency persists in old juveniles. Young also tend to void soon after nursing.

During the first few days of its life an infant may attempt to feed from adults other than its mother. In one observation, a one-day old vicuña put its head under the belly of a pregnant female. She walked away, but the juvenile followed and twice more thrust its muzzle under her belly. Finally the infant turned back to its mother, which was walking a few yards behind, and nursed. Old juveniles that approach strange adult females are met with hostility.

Although there is no strong tendency for juveniles to nurse immediately after rising in the morning, they often do so. In an observation made one morning in April, two females of a band first stood up at 5:30 a.m., shortly before sunrise. Two minutes later a juvenile rose, nursed, and again lay down. Then another juvenile stood up, the adjacent female rose, and the youngster nursed. Inasmuch as the first daylight nursings are no longer or more vigorous than nursings later in the day, young vicuñas probably nurse at intervals during the night.

Rate of nursing.—The daily rate at which the young vicuña takes milk changes as the animal grows, for its stomach capacity enlarges and the amount of solid food eaten increases. On the day of its birth the infant nurses for long periods at frequent intervals. Approximately half an hour after one was born it first put its head under the belly of its mother, as if trying to nurse. An hour after birth it nursed for a period longer than one minute. Then, at intervals of 16 and 50 minutes, it sucked for periods of 1.5 and 2.5 minutes, respectively. Another newborn held its head under the belly of its mother 5 times, for periods as long as 1.25 minutes, in the course of a quarter of an hour. Seven minutes later it sucked for 2.75 minutes, and half an hour later for an equal period.

The duration of the periods of sucking changes little after the juvenile is 2 days old. On the other hand, the interval between feedings lengthens gradually during the first week after birth. These periods and intervals vary in an irregular manner. For 3.5 hours one morning I watched a juvenile which was almost 2 full days old. It nursed at intervals of 10-42 minutes for periods of 2-3.25 minutes. Nine feedings by 3 juveniles, 3 days of age, occurred at intervals of 15-55 minutes. The longest sucking period was 2.5 minutes. At 4 days of age one nursed 6 times at intervals of 9-28 minutes. One 6-day old nursed 3 times at intervals of 45-90 minutes. After it is one week old the juvenile nurses at intervals of approximately 1.5 hours for periods of about 2.5 minutes.

Juveniles still nurse when they are several months old. Then the interval between feedings may exceed 2 hours. Many times in December, and several times in January, I saw a vicuña about 10 months old nurse in typical fashion. The latest date that I saw a yearling nurse was February 21. At Huaylarco, the cessation of the nursing of young occurred in the same month that the first new young were born (February).

Non-nursing relations.—The reactions of the mother to her newborn young are not strongly expressed. During the birth I observed, the mother only once looked back at the emerging fetus. After the infant is born, but before it can stand alone, the mother nuzzles it every few minutes. She does not give it a general grooming. Mother and young spend much of the next two hours lying side by side. Occasionally the mother rubs her head on the juvenile, noses its side, rump, or belly, or licks its muzzle. When the newborn can walk, it may initiate mutual caresses by nosing the head of its mother. An hour after birth one infant straddled the head of its mother as she drank. During the day of the birth mother and young remain together, rarely more than 10 yds apart, and the two generally keep at a short distance from the rest of the band.

In the event of strong alarm, the mother may temporarily leave her infant. One time I walked up to a newborn juvenile in order to photograph it. As I neared, the mother walked away from the youngster and stood at a point 100 yds distant. Five minutes later I departed, and soon thereafter the mother walked slowly toward her youngster. She did not go directly to it but walked past at a distance of 30 yds, halted at a point about 50 yds from the infant, and stared at it. She stood there about 10 minutes. Then when the young one struggled to its feet, the mother

quickly walked to it and led it away up a slope. On an occasion when 14 condors perched near a newly born vicuña, as if to attack it, the mother remained beside her infant until the birds departed.

Even at one day of age, the infant gambols around its mother and dashes ahead when she walks. Often the young one rears up, raises its forefeet off the ground, and puts its chin or neck over the neck of its mother. Commonly, a resting juvenile leans against its prone mother. In one observation, a 9-day old vicuña rubbed against its resting mother, straddled her back with its forelegs, rolled by her side, and jumped into the air as if bucking. Then, tail up, it dashed this way and that close by.

Although the juvenile plays with its mother, she takes small part in this activity. Even when the infant licks her face and nose, the mother usually remains calm and continues to chew cud. On occasions mother and juvenile "kiss" for several seconds, their muzzles nearly touching, their tongues going rapidly in and out. Sometimes the mother licks the head or neck of her infant, or she noses its rump or belly and causes the young one to raise its tail high.

Until the infant is several days old, mother and young usually remain at a distance of about 50 yds from the rest of the band, and the two stay together most of the time. The fact that they stay together is the result of the action of both mother and young. Often the youngster lies down near its mother as she grazes or rests. When she moves away, the juvenile soon rises and follows. If the mother runs, her young one runs with her. On the other hand, sometimes the juvenile wanders away from its mother, and she follows it. In one observation an older juvenile chased a tiny infant. At this, the mother of the infant ran toward it, but before she arrived at its side the youngster ran to another adult. The mother then ran to her infant. Especially when there is some alarm, mother and young stay close together. They are the first members of the band to retreat, and they move farthest away from a disturbance. Indeed, when the disturbance is mild, the mother and young may be the only members of the band that retreat. If there is more than one young juvenile in a band, these young commence to associate with each other, rather than with their mothers, before they are a week old.

At night, or during a hailstorm, mother and juvenile typically lie side by side facing the same direction. This association continues until the juvenile is at least 8 months old. When a hailstorm struck a band which included juveniles 2 and 5 days old, one infant lay crosswise behind its mother, while the other lay several feet from its parent but beside a boulder (similar protection?). At 6 weeks of age juveniles sometimes remain distant from their mothers for periods of half an hour, and the mothers show no apparent concern. At 3 months of age young show little tendency to graze near their mothers.

RELATIONS BETWEEN OTHER BAND MEMBERS AND THE JUVENILE

Adult females and the juvenile.—During the first hour after a mother gives birth, other females of the band inspect the newborn. They approach cautiously, necks craned, and put their noses close to the muzzle, head, side, or rump of the infant. This action of the females is perhaps one of curiosity, similar to their inspection of an adult female that joins a band, but no animosity is shown toward the newborn. The mother seems to take no interest in these actions of the other females. The young one usually tolerates the nosings, but it may pull its head away or walk off. These attentions to the newborn continue for several days.

Commencing when the juvenile is but a day old, whenever it ventures within a distance of a few feet from a band female, not its mother, the adult drives it back by quickly turning her head toward it, and sometimes by spitting at its head or by kicking at it. Often the infant seems to expect hostility, for it raises its tail vertically when it walks close past an adult. By the time the juvenile is several days old it is apparently conditioned to the animosity of adults. It retreats from females that merely reach their muzzles toward it and does not approach them again soon.

As if seeking to recognize its mother, a juvenile may put its nose near the tail of an adult female, especially one that is voiding. As all females except its mother react to this with hostility, an infant probably can find its mother by trial and error and does not necessarily have to recognize her by sight or smell, although such recognition would reduce mistakes. In one observation, a juvenile 3 days old walked close to a pregnant female. She blew at it and the youngster retreated. Three more times the young one approached and the female repulsed it, once chasing it several steps. The juvenile then ran to its mother and nursed. Sometimes a juvenile is repulsed by 2 females in turn before finding its mother.

When juveniles are several weeks old, they seldom nose adults other than their mothers. Adult females, however, may nose young other than their own until the young are several weeks old. Apparently this nosing serves for olfactory recognition, because on occasions a mother noses other juveniles before finding her own.

As juveniles grow older, they are treated more and more like adult females by the adults of the band. If a youngster walks close behind an adult female, she may kick toward it, and if young gambol close to a female, she may spit at them. On rare occasions an adult female seemed to be excited by the play of juveniles and joined them for a short period. One evening in April I was watching 4 juveniles run about playfully when a nearby adult female suddenly jumped up and to the side, as if dodging a bee. She repeated this dodging several times, especially when the juveniles ran close to her. Finally she ran with the youngsters for a minute, often taking big jumps or quick turns to the side.

Adult male and the juvenile.—The adult male of the band, as well as the females, may nose a juvenile a few days old and elicit no more response than the raising of its tail. A different reaction of a male to a one-day-old juvenile was once observed. The suck-

ling stopped nursing as the male approached. The male spit into the air in one direction and another, nosed the base of the tail of the youngster, and then appeared to bite its ear. The juvenile ducked its head and retreated to its mother, which then stood stiffly, rump toward the male, tail vertical. Again, a male chased a 3-day-old juvenile about 15 yds before the mother overtook her young. Commonly a band male spits at juveniles that walk close to him.

Between the ages of about 3 and 10 months, young vicuñas may assume a peculiar attitude when they are within a distance of several feet from a family male. The youngster holds its head high and drawn far back, so that the neck is bent in an *S*, holds its tail up and forward so that the dorsal surface is appressed to the sacral region, and walks slowly and stiffly with legs partly flexed. In mild form the stance may be assumed by a juvenile when it runs into a group of adults, or close to a female other than its mother.

In three observations, a youngster passing close to an adult male flexed its legs so much that it staggered and fell to its wrists and knees. Then it struggled to its feet and walked on. This action suggested that reaction to the adult male had caused an actual block in the nervous system of the young one. Although the adult male elicits this reaction, he himself may appear not to notice the nearby youngster. On occasions, however, he lunges at it with his head, or he takes a quick step toward it, and the juvenile scampers to its mother or to the family group.

Family males were not seen to drive from their bands juveniles that had become yearlings. Apparently yearling males leave the bands before the adult male becomes very hostile toward them. Neither does the family male actively prevent juveniles from visiting other bands. In one observation, though, 2 juveniles walked away from the family cluster while the male was at a distance, chasing another male. The band male made a feint at chasing the youngsters and they raced back to the group. Of course, this is the normal reaction of young in alarm.

Relations among Juveniles

In the first few days of its life an infant rarely seeks the company of other young. Unusually close association of juveniles is shown by the following examples. During a long period of observation of two juveniles, 1 and 3 days of age, they once lay prone as little as 8 ft apart. The next day, when the older infant approached the younger and lay down, the latter rose and walked away, and the two remained at least 5 yds apart. But when these youngsters were 7 and 9 days old they sometimes lay down alongside each other. A few weeks later, when that band included 4 juveniles, the youngest 3 weeks old, all of them sometimes rested together within a space 5 yds in diameter.

A juvenile that is a few weeks old may nose the face, head, ears, or body of one that is a few days old. In one observation, for several minutes a juvenile followed and nuzzled an infant but one hour old. In response to nuzzlings an infant may shake its head or raise its tail, or if lying down, it may stand up, but often it shows no reaction. On one occasion I saw a youngster chase a smaller one for a distance of 30 yds before the mother of the fleeing infant overtook it. On another occasion, three juveniles a few weeks old seemed to be afraid of a new infant in the band, for they ran a few steps away when it neared them. At about one week of age the infant becomes one of the group of juveniles in the band. These often graze and rest together about 50 yds from the adults, and they play together.

A group of juveniles may play continuously for as long as 10 minutes. Periods of play are most frequent, vigorous, and prolonged in the late afternoon. Among young vicuñas play consists of chasing and play-fighting, either usually leading to the other. Often a group of young run away from the adults and back, several times in succession, one then another in the lead. At two weeks of age the young rarely race more than 50 yds from the family group, but at one month of age they run away as far as 100 yds, and at several months of age, twice as far. On occasions the galloping youngsters make high leaps over rocks, ditches, or other obstacles. Sometimes a juvenile acts as if chasing an invisible partner, running fast and recklessly, jumping high, and kicking its hindfeet back. After jumping down over a bank, one fell and turned a somersault. Another fell on a road and skidded along on its side.

Play-fighting, consisting of wrestling with the necks and gentle biting, was observed between 2 infants only 4 and 6 days old. At 3 weeks of age youngsters play-fight by biting each other's legs, kicking, rearing and mounting. At the end of the fight, the contestants usually graze peacefully a few yards apart.

On occasions a juvenile noses the rump of another that is voiding. If one accidentally jostles another, the latter may spit at the head of the first, and the first may spit back. These acts resemble the reactions between the females of a band.

Relations among the Females of a Band

Although on occasions one female of a band acts with hostility toward another, I was not able to discover by field observation any hierarchy of dominance among the established females of any band. However, the established females treat a joining one with hostility, and they treat a new member of the band as a subordinate. In general, my observations substantiate the theory that, in species where social cooperation is highly advanced, social dominance is not pronounced (Dice 1953:281).

Whenever one band female approaches to a point about 5 feet from another, the latter reacts by spitting at the first or, more rarely, by kicking at her. Approach from the rear is especially provocative. If a prone female is closely approached, she may rise quickly, take a few steps forward, and spit into the air. In one observation a female spit at the head of another, then put her muzzle closer and closer, spitting, until her mouth touched the snout of the other as if to bite it. At this action the second spit

into the air, kicked back with one hindfoot, and shook her head.

Sometimes a female evokes the hostility of another by nosing her rump. One put her nose close to the tail of another, which was urinating, then quickly turned her head away as the second spit at it. In another observation the nosed one kicked back with one hindfoot, then both stood tensely for a minute before walking away.

A few times I saw an adult female bite another. While a band was walking up a slope, a female twice reached out with her open mouth as if to bite the neck of another which walked alongside her. One of these two females then chased the other a short distance. In another observation, one female spit at another and pushed it with her chest. Close together, they turned in a circle, and one bit the neck of the other.

On the rare occasions when adult females fight each other, the action is usually short and harmless. The st vigorous fight observed between band females ccurred in December. One put its head over the base of the neck of the other, the second curved her throat over the nape of the first, and the two wrestled with their necks. One reared up and clasped the back of the other with her forelegs, but her grip slipped down around a hindleg. They reared, one at a time, a few feet apart. Again they reared, this time entangling their forelegs. In another observation (April) a frolicsome female, after playing briefly with some juveniles, reared up and clashed with another female. The latter soon pushed the first to the ground with her neck.

MALE TROOPS

Composition.—Male vicuñas that are not members of family bands join together and form troops, which consist of many males without a leader. Judging from many attempts to classify the age of males in large troops at Huaylarco in summer, approximately 80% of the members were yearlings, 10% were two-year olds, and 10% adults. Of the adults, some were cripples and others perhaps weak or old.

Large troops that contained more than 40 members were seen at widely separated localities in Peru. In traveling 17 miles of the road between Chalhuanca and Púquio I saw troops of 20, 33, 45, and 46 members. The largest troop that I observed contained 75 individuals (Huaylarco, January 12, 1952). This number built up during one day through the agglomeration of smaller groups. Then, within a few hours, the big troop was split up by the attacks of territorial males.

Although troops may be large at any season, they tend to be largest during the first few months of the year, for in that period yearling males are leaving family bands and joining troops. At Huaylarco, juveniles began to join troops in November. In mid-November one troop of 7 members contained 2 juveniles, a troop of 28 members had 4, and a troop of 33 had 5. In November, then, both bands and troops may contain juvenile members.

At Huaylarco in early January new yearlings, the old juveniles of December, constituted about 10% of the membership of troops, but there was much variation in the proportion of yearlings in various troops. In one troop, for instance, there was but one yearling, while in some troops of 20 to 40 males as many as 25% were yearlings. By the end of January the proportion of yearlings in troops had risen further. On January 26 I saw 17 yearlings in a troop of 43 members, and on January 29 I saw at least 10 in a troop of 28. By mid-February half or more of the members of many troops were yearlings. For example, there were 7 in a troop of 19 members on February 14, and 17 in a troop of 22 on February 17. My last observation of a male yearling that had not yet left its family band was on February 22, several days after the first juvenile was born near by.

Movements.—The roaming of a troop of males seems to be directed primarily by food-seeking. Thus the limits of the area over which a troop wanders would seem to depend largely upon the limits of an area of suitable food. Such an area might be the flats and gentle slopes in the vicinity of a stream and its tributaries. Inasmuch as herbage and topography are not uniform over a region, it is not known whether troops would be nomadic under uniform conditions. Studies of the movements of marked animals are needed.

For periods of a day a large troop may move no more than a resident band. In one observation, a troop of 30 males remained within an area of 400 x 600 yds for 2 days, in spite of several attacks by territorial males. Again, 51 males stayed within an area of 60 acres on poor pasture for a period of 5 hours one morning. But on the other hand, a troop sometimes moves fairly steadily in one direction for half an hour or longer. I noted that one large troop moved three-quarters of a mile in 40 minutes, although no alarm was apparent. Generally these long movements lead from one grazing area to another across a more barren zone.

For a period of 4 days I kept track of the movements of a troop of males at Aricoma. The observed movements are diagrammed in Fig. 16. In their erratic course, the animals walked or ran a distance of more than 10 miles, but all of their wanderings took place within an area of less than 2 sq mi.

Leaving and joining.—In the foregoing observation, for the first 2 days (July 5 and 6) the troop numbered 31 males. On the morning of the third day there were 30, but that afternoon the troop was split into groups of 11 and 19 members. The following day 4 males departed from the 19 at about 10:30 a.m., the main group increased to 21 members by 1:00 p.m., and then decreased to 19 again at 2:30 p.m. On the fourth day at about 10:00 a.m. the membership increased from 19 to 26 males, and this number remained in the group the rest of the day.

The major split of the troop of 30 males into 2 smaller groups was brought about by the aggression of 3 family males, which herded the troop up a rocky

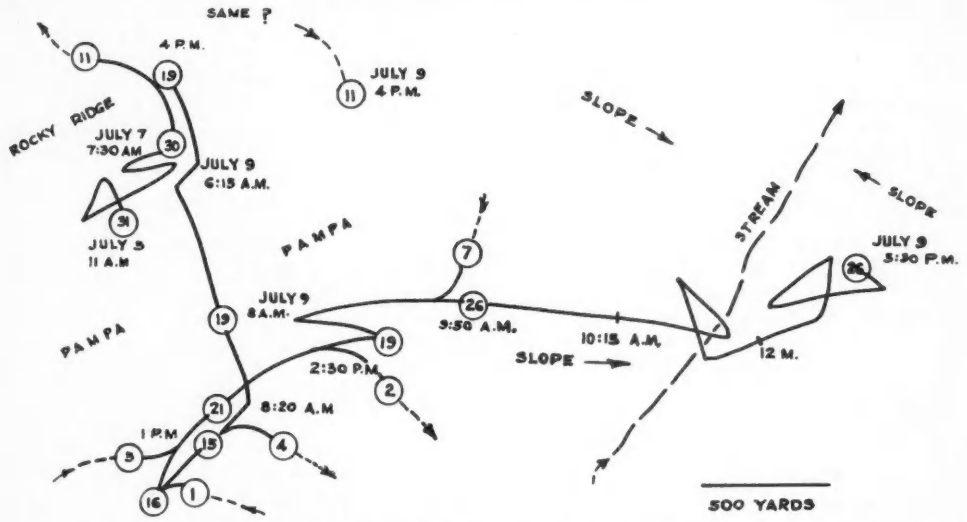

FIG. 16. Diagram of the movements of a male troop during a period of 4.5 days. Circled figures are numbers of males in the troop. Solid lines show direction of major movements, starting at left center (July 5). Arrows indicate members joining or leaving troop.

ridge. The other losses of members occurred when a few individuals wandered off. Some of these walked steadily away as if headed for a distant goal. Others departing soon encountered family males which chased them farther from the troop.

Apparently the troop is an open society which immature and some other males can join and leave without causing much reaction among the members. A joining member normally elicits only the stares of a few troop members. Here is an example of the joining of troops. One morning troops of 16 and 19 males grazed 0.25 mi apart. In the course of foraging the two groups slowly came together. As they merged one male retreated a few yards with tail up, and several others stared at the opposite group. But then all grazed peaceably as one troop of 35 males. Twenty minutes later, as this troop drew near a troop of 10 males, a member of the big troop ran to a point a few yds distant from the small troop, then retreated as a male of the latter troop ran toward him. There was no further animosity.

On occasions, when a few immature males approach a troop several members run toward them a short distance, but troop members seldom inspect closely a male that joins them. (Band females, however, intimately inspect joining females.) A joining male acts aggressively only when he is met with hostility. In one observation, an immature male was grazing alone when a large troop neared. He ran toward the group but quickly turned away as three troop males dashed toward him. Then he jumped atop a boulder and kicked at the aggressors.

Cohesion.—Males stay together in a troop because of their gregariousness and mutual tolerance. Frequently 20 or more males stay together for a period longer than one day. When a troop moves a long distance a few members sometimes loiter as far as 200 yds behind, or even lie down, but these soon run to catch up to the main body. In spite of these evidences of cohesion in a troop, part of it may readily be separated from the rest. On occasions I saw part of a troop walk in one direction, while grazing, and the remainder walk away in the opposite direction, splitting the group. One observation illustrated both cohesion in a troop and the lack of it. During a period of 4 hours one morning, a troop of 51 males grazed on a pampa, half a mile distant from the foot of a steep barren slope. Then 45 of the males walked slowly to the foot of the slope and grazed there. Within the next half hour, 24 of the males ascended the slope and walked away along the crest. A quarter hour later the rest of the 45 followed the same course. But 6 members of the original 51 still grazed far out on the pampa and did not join the others.

In alarm troop males react like band females; that is, at a sudden disturbance they concentrate into a tight group and flee together. On an occasion when I drove my car along a road between two parts of a large troop of males, all the members of one contingent tried to run across the road ahead of the car in order to join the other group.

Males of a troop are also like the females of a band in that they are intolerant of the close approach of fellow members. A male spits or kicks at another that comes within a distance of a few feet, especially if the approach is from the rear. On the whole, however, troop males show greater mutual tolerance than band females. Another point of difference is that among band females the action of nosing the anal region of another is rare, but among troop males this action is common. For example, in one observation a male approached another which was voiding

and nosed the base of his tail. The voiding one spit at the first, then raised his tail higher. Three times the nosing and consequent spitting was repeated.

Many factors influence the frequency of changes in the composition of male troops. Where there is frequent disturbance by man, livestock, or family males, the membership of a troop may change several times a day. The attacks of territorial males often split up troops, but the action of these males in herding small troops this way and that sometimes brings these groups into company and amalgamates them into a single large troop. Alarm speeds the formation of large troops because in alarm troop males aggregate. But with increase in the size of a troop the opportunities for separation of a part are increased, so troops of hundreds of members are not built up.

Because the composition of troops changes often and that of bands seldom, it would appear that troop males tend to stay together less than band females. But it difficult to make a fair contrast of the cohesion in troops and families for a troop, as compared to a family, has a large number of members, an extensive and therefore relatively unfamiliar feeding range, and a lack of leadership.

Play-fighting.—The immature males of a troop, like the juveniles of a band, frequently play-fight among themselves. This play is most frequent in the late afternoon, after 4 p.m., and it may continue until dark. The method of play-fighting is about the same as of fighting between adults, but play-fights are gentle and frolicsome for the most part. In a play-fight two adversaries feint, fence, push, and wrestle with their heads and supple necks. Each strives to put its neck over that of its opponent. The contest consists mainly in striving for this advantage and in thwarting the attack of the other. Inasmuch as a high reach of neck and head is an advantage, one may rear to get its neck uppermost, or both may rear and strike their chests and flexed forelegs together. The advantage being gained, the upper one brings his neck down atop the neck or shoulders of the other, perhaps raising his forelegs to bring his weight to bear, apparently trying to force the second to its knees. At this point both animals sometimes drop to their wrists and the bout ends.

An alternate attack is for one to put its head under the chest of the other and trip one of his forelegs. To counter this attack the defender draws the leg back, or he flexes both forelegs and drops to his wrists. Eventually one may lie prone so that the head of the other cannot be thrust beneath his body. But if one lies down, the other may nip his heels or head, or straddle his back.

During a play-fight the mouths of both contestants may be constantly open, ready to bite, and commonly one bites the wrists, heels, or neck of the other. Probably these bites are harmless, for the caniniform teeth of immatures are tiny or absent. In the course of a fight one vicuña sometimes pushes his chest against the side of the other's, as if to knock him down sideways. Again, one clasps his forelegs around a hindleg of the other, or one mounts another and remains astraddle for as long as a quarter minute. A play-fight occasionally becomes vigorous. In one energetic fight grating cries were almost continuously given, and at the end one contestant held its muzzle high, a tuft of hair in its mouth, and spat 3 times into the air. The other members of a troop may watch an especially active contest, but usually they pay but slight attention to a play-fight. On rare occasions a third young male joins in a play-fight between two others. At the end of a vigorous fight the adversaries stand stiffly a few yds apart, lips agape as if with panting, and soon they lie down to rest.

Among troop males, as among juveniles in a band, play-fights are broken by periods of chasing. In a vigorous chase the pursuer extends his lowered neck so as to bring his head near the side of the fleeing one and attempts to trip its hindlegs. When closely pressed the pursued vicuña kicks back at the head of his pursuer, but the blow rarely strikes. To avoid this kick the chaser pulls his head up and back, and in doing this he loses speed and falls several yds behind the pursued one.

TERRITORIAL AND INTERGROUP RELATIONS

The area that an animal defends against members of the same species is its "territory." In birds, the animals in which territoriality has been most studied, the territory is usually defended by the adult male and principally against other males. In much the same way vicuñas are territorial. Throughout the year a resident male vicuña defends the home range of his band; that is, he drives other males from the area in which his band normally grazes, rests, and cares for the young.

DEFENSE OF TERRITORY

Area defended.—In strict sense, I consider a vicuña territory to be the area that a resident male defends against other family males (Fig. 17). This area can be delimited accurately only by observing the points that an intruding family male must cross, within sight of the resident male, before the latter makes a sortie. The mere fact that a band is found at a certain place does not mean that the site is within its territory, because for several hours after a disturbance a band may graze on unclaimed ground or in the territory of another. Neither does the observation of a family male attacking a troop of males surely indicate that the site of the encounter is within his territory, for such attacks may continue far beyond territorial limits.

In spite of these difficulties, in a single day of observation one can discover the location of many segments of the mutual boundary line between two territories. This is possible because most encounters between neighboring band males take place where their territories adjoin on areas of favored pasture, not along the entire peripheries of their territories. Of more than 100 encounters observed between bands A and B, which had a mutual boundary line 300 yds in length, about two-thirds of the meetings took place at two segments of the line, each approximately 25 yds long,

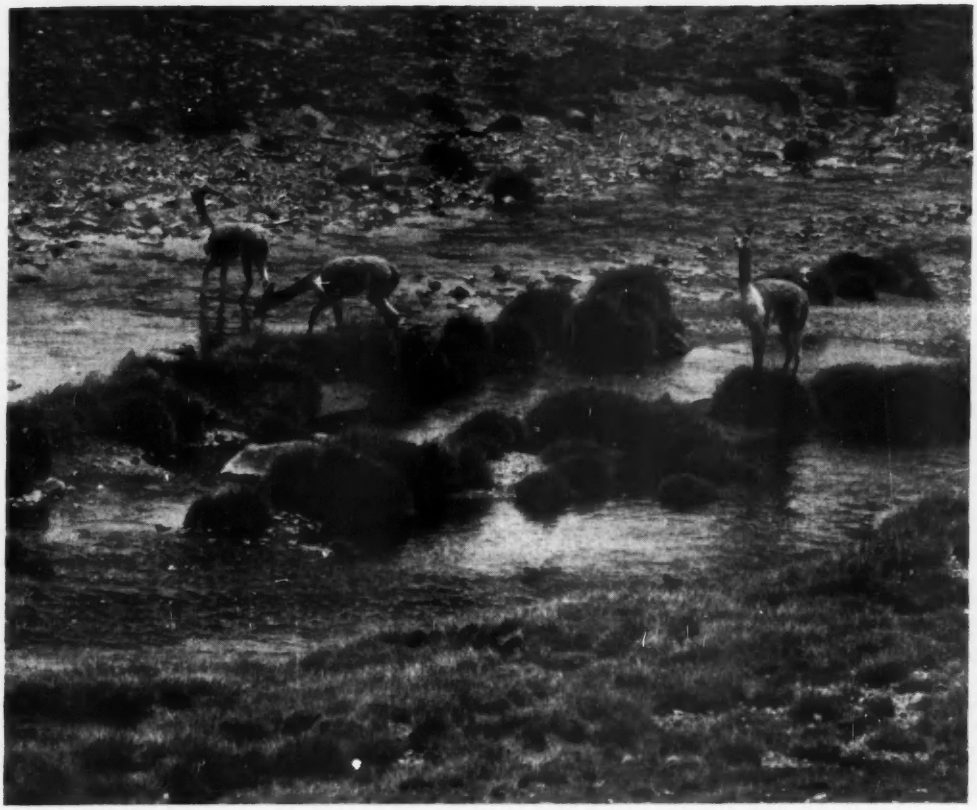

FIG. 17. Territorial boundaries frequently coincide with the location of streams. Here an adult male displays and drives off two intruding vicuñas, which retreat submissively. Huaylarco, Arequipa; February 25, 1952.

where the boundary crossed preferred grazing sites. The majority of the encounters observed between groups that inhabited large territories on rather barren ground occurred at a few sites where the forage was attractive.

On the other hand, the entire periphery of a territory can seldom be discovered through observation of the encounters between family males alone, for a territory may never be invaded by alien family males from certain sectors, such as where barren ground adjoins the territory. In practice, however, I found that a resident male normally made his initial attack on approaching troop males at the territorial boundary. And as troop males often entered a territory from undefended areas, many points on the territorial boundary could be determined by observing the initial attacks of a resident male on invading troop males. In addition, when the same band was found repeatedly at certain sites it was assumed, and frequently confirmed, that these sites were within the territory of that band. Barring disturbance by other animals, the vicuñas of a band normally remain on their territory.

The best time of day for finding a band on its territory with all members together is about sunset, when diligent grazing is the principal activity of vicuñas. Observations of resting bands before they first rise in the morning are very useful in determining points within territories, but only when verification can be made on different days, for disturbance during the night may cause a band to move out of its territory. I learned the approximate boundaries of the territories of 3 bands at Aricoma and 18 bands at Huaylarco. The territories at Huaylarco, as determined by observations from November through April, are mapped in Figs. 18 and 19.

The areas that are not included in vicuña territories are called "unclaimed ground." This ground includes rocky ridges, rock slides, upper hillslopes, and barren pampas, all of which are unsuitable for sustained grazing. Displaced bands may graze on unclaimed ground before they return to their territories, and troop males may graze there when kept from better pastures by the animosity of resident males.

Display.—Family males are intolerant of all other males except the young ones of their own bands. As in birds, fish, and other vertebrates in which territoriality has been studied, encounters between male

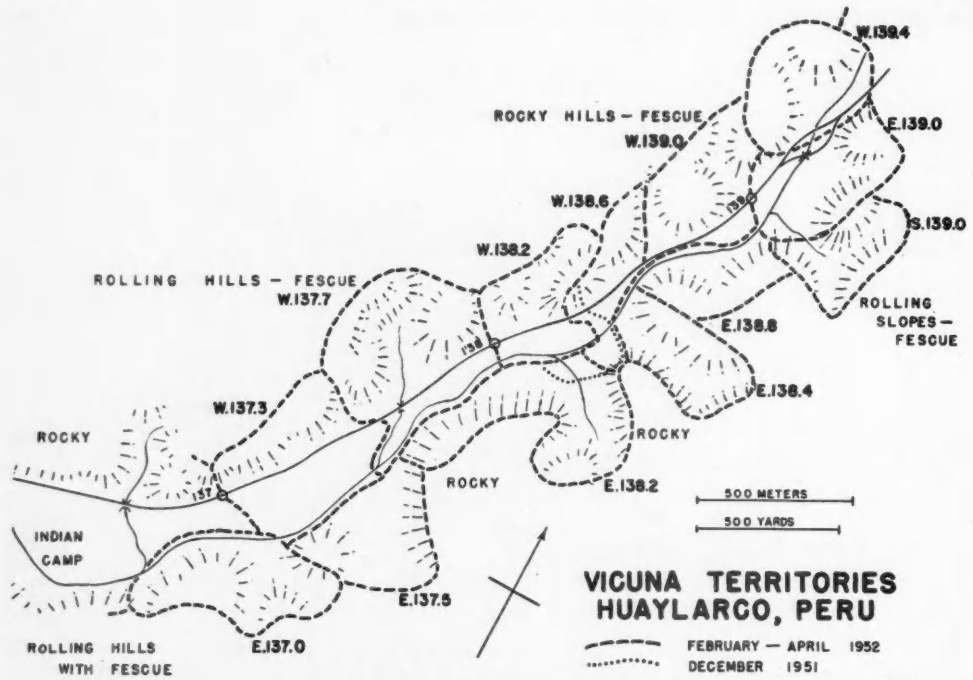

FIG. 18. Map of the vicuña territories of the eastern part of the study area at Huaylarco, February-April, 1952. The area lay along both sides of a shallow stream valley and dirt road. Numbered circles on the road indicate kilometer posts on Arequipa-Puno road. Territories, shown by heavy broken lines, are designated by a letter and 4-digit number. Dotted line indicates territorial change explained in text.

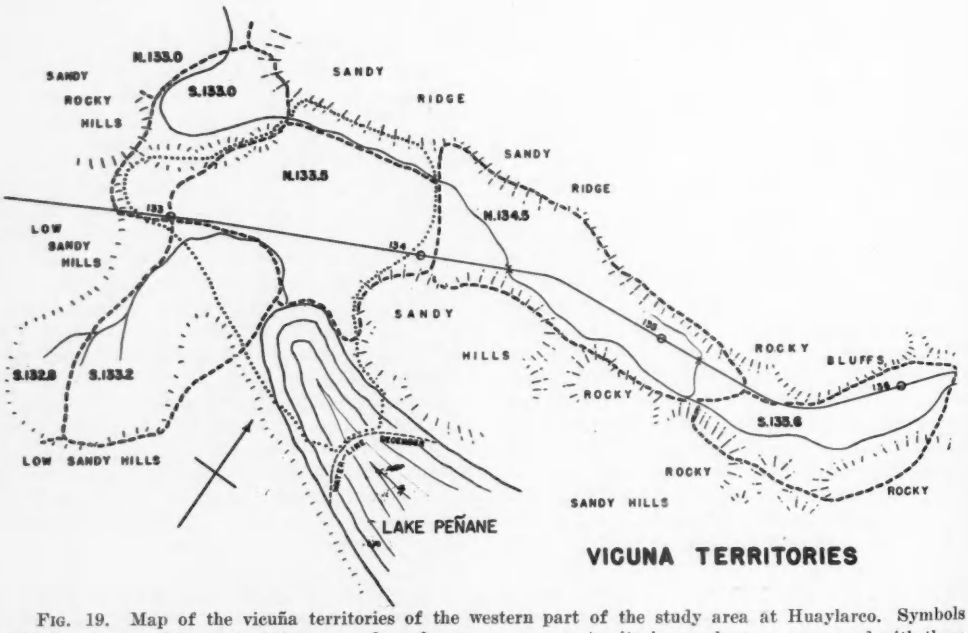

FIG. 19. Map of the vicuña territories of the western part of the study area at Huaylarco. Symbols as in Fig. 18. In this part of the area, where forage was sparse, territories are large as compared with those of the eastern part, where forage was abundant.

vicuñas consist principally of aggressive display and pursuit, rarely of actual fighting. A common feature of male display in vertebrates is that the displayer makes himself appear as large as possible. The male vicuña does this by standing stiffly erect with neck and head high, ears up, and tail erect (Fig. 2). The effect of tallness is increased when the male stands on a tuft of grass, dung pile, boulder, or other prominence (Fig. 17). Again as in the display of some other vertebrates, the male vicuña frequently presents his side toward the object of the display. This position not only enhances the appearance of large size but puts the animal in readiness to dash away. In strong display the tail stands vertically, its white under surface perhaps acting as a visual warning signal to other vicuñas. In mild display the tail is held but slightly out from the rump. There are probably many subtle forms of display that are obvious to vicuñas but not to the distant human observer.

The male prances as he walks in display. And as he runs to attack he usually keeps his head very low, below the level of his back. In this pose a vicuña somewhat resembles a hound following a trail of scent on the ground. A vicuña retreating submissively from an aggressive male assumes a subordinate attitude with tail down, head slightly lowered, and ears depressed.

Relations between Family Bands and Male Troops

Belligerence of family males toward troop males.—When a large troop of males moves toward a resident band, the usual sequence of events is as follows. The band male stares at the troop from time to time and gives the alarm trill. If the troop continues to approach the resident male walks or runs about 50 yds toward it, and stands in aggressive display. After a few minutes he may return to his family, but if the troop moves still closer he makes a sortie. At first he walks toward the troop, stopping to defecate on the way. Then he gallops, halts, stands in display, gallops on, and finally stops at a point about 20 yds from the troop and displays strongly. If this last warning fails to turn the troop, the male attacks.

In attacking a troop the aggressive male chases one or a few individuals at a time. He may take only a few steps toward them, or make short dashes or feints at attack. But again he may chase one for several hundred yds, through many sharp dust-throwing turns, giving high wavering screeches from time to time and hoarse growls when pursuit is close. Although the male appears to be in deadly earnest in these chases, he rarely touches his quarry. He may not close the distance to less than a few yds even when he chases a single vicuña vigorously for several minutes.

Instead of attacking the nearest members of a moving troop, the hostile male sometimes dashes past the main body and chases those in the front. On occasions the van may excite stronger antagonism than the rear because it is farthest into the territory of the male, but this is not always the case. At other times the attacker drives a few members far ahead of the troop, then returns to chase the others in the same direction. In some observations, half of a large troop was herded 100 yds ahead of the remainder before the male went back to attack the rest.

As the troop moves away from the territory of the male, his charges grow more infrequent and he guards the troop from greater distances. Seemingly the impulse to stay in his territory conflicts with his urge to attack the troop, the result being that a family male rarely follows a troop more than 300 yds outside of his territory or, under these circumstances, stays outside of his territory for a period of more than 10 minutes.

A resident male will attack a troop of males that crosses his territory in fleeing from a man or a dog, provided that the cause of the alarm is hidden. Apparently, then, there is no contagion of the fleeing reaction from an alarmed troop to a family male. In one observation, a troop of 25 males ran over a ridge into a territory. The resident male gave a cry, attacked the troop, and drove it slowly back over the ridge. Then he stood atop a rock halfway between his females and the retreating troop, but suddenly he galloped away, accompanied by his family. Atop the ridge appeared the cause of the troop's alarm—a man.

Although troops usually enter territories to reach good pasture, many invasions of territories by small groups of immature males are brought about by their tendency to join groups of females. As females are not hostile toward troop males, a troop may graze very close to a family while the band male is absent. If he is present, however, he quickly recognizes any foreign male that approaches and drives him off. The actions of troop males in joining band females, and the reactions of the band male, are illustrated by these examples. The male of a band stared at a troop of 15 males that stood 50 yds distant from his family. When one of the 15 ran toward the cluster of females, the family male intercepted him and gave chase. The rest of the troop males then ran to the females. For 5 minutes the resident male vigorously chased the intruders, while his females stood together a short distance from the scramble. On another occasion, a troop of 8 immature males stood 50 yds distant from a family band and the band male did not attack them. But then, 3 times within a period of 10 minutes, one of the young males walked toward the group of females and the family male chased him off. Again, 2 immature males entered the territory of a large band and 1 was attacked by the resident male, but the other ran to the group of females. The adult male galloped back to his family and drove off the intruder.

Point of attack.—Usually a band male does not attack a troop until it crosses the boundary of his territory, but after starting to attack he may continue pursuit outside of his territorial limits. These facts are illustrated by the observation following. A resident male occasionally stared at a troop of 19 males that grazed on the opposite side of a stream and a road which lay near his territorial boundary. Soon 4 males of the troop crossed the road and entered his

territory at a point 250 yds distant from him. He ran toward the troop, paused at the edge of the stream, stared at the intruders, crossed the stream, attacked the troop and pursued it across the road. The troop fled uphill 75 yds ahead of the hostile male. He followed to a point 100 yds outside of his territory. Then he displayed near the troop for several minutes, drove it onto a hilltop, and returned to his family. In many observations, a resident male allowed a troop of males to cross barren rocky slopes on unclaimed ground bordering his territory, but as soon as the troop descended into the territory the male attacked.

Effects of attack.—A single belligerent male can drive a large troop a distance of 300 yds in 5 minutes of pestering. One herded a troop of 21 males a distance of half mile in 25 minutes. Another maintained an attack on 26 males for half an hour, alternately chasing them and standing in display. In one observation, a single family male split a large troop. A troop of 33 males was walking east when a family male ran to a point in front of them. The leading 15 males turned back to the west. The aggressive male stood nearby for a few minutes, then chased four members of the troop past the others. He stood in display as the remaining 11 walked and ran close past him. Next the hostile male ran back to a point 20 yds distant from the eastern contingent of 18 and displayed. A few minutes later he ran 10 yds closer to the group; it retreated. Once the western group turned back to the east, but the male dashed a few yds toward it and the group turned away again. Urged by the male, which displayed and sometimes gave chase, the contingent of 18 continued on eastward. The entire action took place in 25 minutes.

The extent of the effect on troop movements of attacks by family males is illustrated by the following summary of the attacks observed on one troop at Aricoma during a period of 4 days. General movements of the troop during this period are shown in Fig. 16.

July 5, 11:00 a.m., to July 6, sunset: Troop of 31 males attacked at least 10 times by male of band A. Each attack moved troop 50-300 yds. Several times aggressive display close to troop by this and another family male.

July 7, 7:30 a.m. to 5:00 p.m.: No attacks until mid-afternoon, for resident band out of sight of troop. When disturbed by Indian, troop moved 300 yds northward, over low ridge, and there was herded high on rocky slope by three family males. Band split in two; larger contingent of 19 returned to near morning site.

July 8, 6:15 a.m. to 4:00 p.m.: 6:30 a.m., male of A chased the 19. By 8:20 a.m. troop had moved 1,000 yds southward. Four males wandered from troop and were chased away by band males. 10:15 a.m., troop of 16 herded by 3 family males. As troop moved eastward through various territories, attacked by at least 5 different family males.

July 9, 8:00 a.m. to 5:30 p.m.: Troop of 19 moved eastward 500 yds down long slope, where 7 more joined. These 26 chased by one family male. 10:15 a.m., troop reached stream in flat green canyon bottom. Attacks of one male moved troop quarter mile downstream in half hour. Another male herded troop back upstream. First male returned to attack, third family male joined in. Troop pushed about for 20 minutes by 3 males. Two members broke away and were chased, but later rejoined troop. Two hostile males herded troop 100 yds southward to foot slope. One attacker departed, another took up attack. Troop moved slowly eastward along sidehill for half hour, one male guarding and occasionally attacking. Several more attacks later in day. Undisturbed, troop tended to go down and across slope to eastward. One attack drove it 300 yds back to west in 20 minutes.

Relations among attacking males.—Two or three family males may attack a troop at the same time. When this occurs, the family males do not cooperate in moving the troop in one direction but each acts independently. In one observation, 3 males stood in display on different sides of a large troop. Whenever part of the troop surged toward one attacker, he drove it back into the confused central mass. On aonther occasion, 3 family males split in two a troop of 31 males by herding the group among rugged barriers of rock.

While pursuing a troop a resident male may quickly break off his attack and gallop off to challenge a family male that enters his territory, especially if the latter approaches his family. In one instance, through long effort a resident male drove a troop of 45 members away from his family and to a point about 100 yds distant. Then a neighboring family male entered the territory of the first. The first male ran away from the troop and attacked the single intruder. On occasions the reverse action was observed; that is, a resident male broke off aggression toward a family male in order to chase an approaching troop. Apparently some intruders excite the defending male more than others, but the one attacked is not always the one nearest to the male, his family, or the center of his territory.

A troop that is fleeing from one aggressive male sometimes enters the territory of a second. Then the first male usually leaves off the chase and the second takes it up. In one observation, a small troop was pursued by 4 resident males, one after the other, during a period of only 10 minutes. On occasions when a troop of males reaches the boundary between two territories, the action among the various males may become complex. A relatively simple example of this interaction is the following observation.

A troop of 5 immature males walked toward resident bands A and B. The male of band B raced 300 yds to chase the troop, which fled toward band A. As the male of B returned to his females, the male of A approached the intruders and stood near them in display. The 5 males stood submissively until the aggressive male came closer; then they walked away toward the territory of B. Soon the male of B attacked the troop and it fled. Again the male of A ran toward the 5. They scrambled up rock slides

onto unclaimed ground and walked across the slope uphill from band B. Band A started to follow the 5 males but the male of B chased it back into its own territory, and then he attacked one of the retreating troop males. The entire action took place in a quarter of an hour.

Variation in tolerance for troops.—Resident males differ widely in their pugnacity toward troop males. The least militant resident male observed was a solitary one which was becoming established in a new expansion of his territory. This placid male lay prone while 5 yearling males played within 10 yds of him. Occasionally he chased them and other small troops of males in a mild and leisurely manner. This male was exceptional; perhaps he was very old. Normally so sure is the attack of the resident male on a troop that enters his territory that the site where a large troop grazes unmolested may be assumed to be undefended, either because it is unclaimed ground or because the resident male is absent.

Even when a band is not on its own territory its male is belligerent toward troop males, and they retreat when he draws near. In one observation, a disturbed band fled out of its territory and far up a rocky slope. To descend to grassland the band had to pass close to a troop of 11 males which stood on unclaimed ground. The family male descended ahead of his females, chased the troop a short distance, and then, followed by his family, he walked downhill to his own territory.

Family males attack large troops more readily than small. Yet a resident male may go far to chase a few troop males. In an observation made early one morning, shortly after rising a band male walked, then ran, toward 2 immature males which stood 500 yds away. They started away when he reached a point 200 yds short of them, but he closed this distance to 10 yds as he pursued them over a ridge. On a sandy pampa a resident male was seen to travel a distance of half a mile in order to chase a small troop.

On occasions, a resident male will tolerate minor invasions of his territory by a small troop, or he delays his attack until the troop has been on the territory for many minutes. In the latter case it is as if the continuous or repeated small stimulus caused by the presence of the troop finally causes a reaction in the resident male; this is somewhat analogous to nervous summation. On one occasion, I watched the male of a band chase a troop of 15 males upslope onto a barren rock slide, then return to his females. The troop did not descend lower, but three-quarters of an hour later the same male attacked the troop again and herded it across the slope. Perhaps the failure of a troop to move away after aggressive display or attack brings on further aggression.

Time of attacks.—Troops may be attacked by resident males very soon after vicuñas first rise at dawn. One winter morning at 6:05 a.m., when sunshine had just reached the highest peaks, the 24 males of a troop were lying on a slope in the territory of a family band which stood a quarter mile distant. As it grazed, the family slowly moved toward the troop, the band male walking 200 yds ahead. He pranced to a point 20 yds from the downslope members of the resting troop. These rose, walked uphill, and stood near the other members. The band male displayed 10 yds distant from the troop, which then walked slowly uphill and away. At 6:10 a.m. of another morning, I saw a male run a distance of a quarter mile from his family to attack a troop of 23 males.

There is a decrease in the vigor and frequency of the attacks of family males on troops late in the day, after 4 o'clock, apparently because the band males are then preoccupied with filling their stomachs. In one observation, a troop of 11 males descended from a barren hillside to the grass of a territory below at about 4:30 p.m. The resident male drove back a few troop males that approached him, but the troop continued to work gradually down the slope in grazing. The family male displayed nearby and finally walked close to the 11, which retreated. But again they descended until at 5:00 p.m. they grazed at the foot of the slope. The resident male did not again molest them.

Interpretation of the observed actions between males must always be cautious because these vary with time of day and season, and the reactions of resident males toward family males and troop males are different. Territorial males may not react the same toward small and large troops, toward young and adult males, and toward all individuals. In addition, the observer has at best an imperfect knowledge of territorial boundaries and of subtle forms of display.

Resistance of troops to attacks.—When a territorial male attacks a troop, usually the members nearest the aggressor retreat and those that are lying down stand up before he reaches a point 10 yds distant. But if a troop has been chased a great deal during the day, it becomes relatively insensible to attack and may not move away until the attacker is less than 5 yds away. On an occasion when a male attacked a troop that was bathing, several members continued to bathe when he was no more than 10 yds distant. Late in the day troop males are sometimes so bold toward a territorial male that he has difficulty in forcing them away from good pasturage.

One observation of unusual resistance of a troop to aggression by a resident male was made during a hailstorm. As the aggressive male approached a troop of several males, hail commenced, and some members of the troop lay down. The attacker displayed close to them, but only one rose. The hail continued and all the troop males lay prone together. Soon the aggressive male lay down 10 yds distant from them. When the hail turned to rain a few minutes later, the band male rose and walked toward 2 members of the troop. They rose and walked away, the family male following a few yards behind, but the rest of the troop remained prone. Several minutes later the resident male returned to these, they rose and walked away, and he returned to his family.

Troop members seldom retaliate when a family

male attacks them, although they may hold their tails up when a male approaches or chases them. If closely pursued, a troop male sometimes kicks back at the attacker, and on occasions when a family male displays close to a troop male the latter may kick toward him. However, troop males are much less apt to kick at family males than at each other.

Reactions of troop males to family males.—As frequently the first reaction of a vicuña to an approaching object is to run toward it, troop males may run several steps toward a family male as he comes to attack them. Then, recognizing the male as aggressive, the troop turns tail and retreats. On occasions when troop males are very bold they may approach close to a hostile adult male. Once I saw 2 males of a troop nose the side of a resident male which stood in aggressive display. With a sudden turn and kick, the big male drove them back. In an observation made late one afternoon, a troop of males descended a slope and were met by the resident male, which ran toward them and stopped 100 yds distant. Five of the troop males galloped forward to a point but 10 ft from the belligerent one. He stalked toward them and they retreated up the slope to their fellows.

The hostile male herds the troop as it retreats. He may walk behind or beside the group, sometimes moving from one side to the other, and occasionally he dashes at laggards or others that stray from the group. This action reminds one of the herding of cattle by a horseman. The aggressive male frequently stands in display and watches the troop walk by. In this action he resembles a proud general watching a group of defeated soldiers straggle past. Whenever a member runs from the herded troop, the aggressive male races after it. In alarm the pursued one tries to rejoin the group, but he cannot return in a direct path without being overtaken. As a result, the separated member may be driven 50 yds away from the troop before he is able to turn back toward it. The path of his flight and return is an approximate circle. Even though an individual or troop is chased but 50 yds, it may continue on for half a mile as if to reach a grazing area where attacks are less frequent.

Apparently the action of fleeing is contagious among males of a troop, for sometimes when only one member is pursued all of them run. Further, troop males may run after an aggressive male that is chasing others of the troop. In fact, a troop male may overtake and even run past the aggressor.

Commonly a troop retreats upslope when attacked. This action may quickly end the pursuit, for the troop moves onto undefended ground. At Aricoma, if a troop of males fled from the territories of bands A or B and climbed 50 yds up the adjacent rockslides, it would usually be safe from attack. An unusual method of escaping attack was once observed. A troop of males fled into a stream. When they started to ascend either bank, a belligerent male drove them back down to the water. Finally the troop walked in the water to a point 50 yds upstream, out of the defended area, and ascended the bank there.

The fact that a family male chases a troop of males does not seem to increase their fear of him, for the troop may return again and again to the site from which it was chased. In a period of one and one-half days, a large troop was attacked at least 10 separate times by the same family male. In another observation, a solitary resident male chased a troop of 40 males over a low hill at 12:30 p.m. An hour later the troop was back again; the male pursued it over the hill as before. By 3:15 p.m. the troop had returned to the site from which it had been chased, but as the resident male was behind a rise of ground, he did not see the troop. Three-quarters of an hour later he spied the troop and gave chase.

The males of one troop showed strong interest in, and apparent fear of, a lone adult male that was so ill he could not stand. With ears up and necks craned forward, several young males slowly walked toward the prone adult from the rear. Most of the young males retired upon reaching a point several ft from the sick male, but, with his nose, one almost touched the tail of the adult. At this the adult made a slight motion as if to rise, and the immature backed away quickly.

When fleeing in strong alarm family bands and male troops may join temporarily. On an occasion when a dog walked near, the 4 members of band B joined a group of 12 running vicuñas, and all ran up a slope. The dog paid no attention to the vicuñas and soon left. Then from the composite group the members of band B and 5 other vicuñas departed. The sex of the 5 was not determined, but the 7 that remained on the slope were males. In another observation, as 2 resident bands ran away from an approaching llama train a troop of 20 males joined them and the composite group ran on.

Reactions of troop males to females and young.—Because vicuñas are gregarious, one or a few troop males may join other groups of vicuñas if they are not met with aggression. Troop males sometimes join a family of vicuñas and graze with them for a short time until they are driven off by the band male. Inasmuch as the band juveniles stay near their mothers while the family male is attacking a troop, small juveniles rarely encounter troop males. In one observation, however, a small juvenile wandered 50 yds away from its mother and approached a group of 3 immature males. With necks craned forward, the 3 males gingerly nosed the youngster. One male put his neck over that of the juvenile, and another kicked back when the juvenile walked behind him. Some time later, 3 juveniles of the same band wandered 50 yds from their mothers. The same troop males walked to these young and cautiously nosed their heads and shoulders. Then the family male approached, the troop males walked away, and the juveniles returned to their family. On another occasion, several members of a troop of males chased for a few steps a juvenile about 2 months old that joined them.

RELATIONS BETWEEN FAMILY BANDS

Attacks on transgressing bands.—A family band normally stays on its territory. But on occasions when one band enters the territory of another the resident male of the latter drives off the invaders in about the same manner as he attacks invading troops of males. The principal differences in the interactions between the resident male and a trespassing band as opposed to an invading troop are: that a band reacts to the aggressive actions of the resident male at relatively great distance, that an alien band may not be entirely submissive toward a resident male, that a band is rarely pursued after it departs from the territory it has invaded, and that a displaced band does not tend to return soon to the area from which it has been driven.

Between the neighboring bands A and B at Aricoma, where the terrain was hilly and the forage good, the greatest distance that the male of one band would run to attack trespassing members of the other was about 200 yds. (Sorties of twice this distance were sometimes made to attack large troops of males.) The members of the trespassing band seldom retreated from the aggressive male until he was about 50 yds distant. On rather barren pampas at Huaylareo the distances of attack and reaction were much greater than among the hills at Aricoma. These differences were probably due to the facts that territories were larger and visibility was greater on the pampas. In one observation, a resident male ran half a mile across a sandy pampa and attacked an approaching band. When the attacker was about 200 yds distant the invaders fled.

As in encounters between resident males and troops, encounters between family bands are infrequent after 4:00 p.m. In the evening bands are grazing diligently on favored sites and resident males are comparatively tolerant of minor infractions of their territories.

The resident male attacks principally the male of a trespassing band. Pursuit may continue for a few steps, or for a distance of several hundred yds, as illustrated in the following example. One afternoon resident bands of six and 26 members grazed 100 yds apart near their mutual boundary line on a pampa. The male of the smaller band occasionally displayed near the larger. Finally he rushed into the large band, but he quickly fled out on the opposite side, pursued by the defending male. Away from the direction of the families the pair ran, at first in a wide arc, then in a straight path for a quarter mile. The two were but a few yds apart when they crossed a road, the territorial boundary of the large band. They continued on for a distance of about 100 yds, dashing this way and that. Then the pursued male halted, his pursuer turned back and ran to his large family, and the pursued one followed 200 yds behind. Both were near their families 5 minutes after the start of the chase. This observation was exceptional in that a family male was chased by a resident male to a point outside of his territory. It seemed that the chase was so heated that the boundary was not strictly observed.

Frequently the attention of the observer was first attracted to a chase between males by their cries. Chases are accompanied by scraping grunts, deep growls, and long wavering screeches pitched about an octave above middle C. The sound of these screeches has the quality of friction between broken edges of glass. In close display males utter bleats, growls, or croaks from time to time. It is seldom apparent which male is making the sound. All of these vocalizations are distinct from the alarm trill.

Encounters between family males commonly end with both standing in display several yds apart. Seeing this action, one cannot help but be reminded of two small boys standing on opposite sides of a chalk line, each daring the other to cross it. While poised thus a male may growl, spit, or defecate. Finally, after standing tensely for about a minute, one male and then the other resumes grazing or returns to his family.

As a male runs away from his family to challenge an intruder, or as he returns from a sortie, he may halt at dung piles and defecate, or at least go through the motions. During some observations of 2 males in display at short distance, one of them ran off to a dung pile as much as 50 yds distant, defecated, and then returned to posture even closer to his opponent. In these instances defecation seemed to be a displacement activity, in the sense of Tinbergen (1952:6), produced by conflicting drives to attack and to flee. This tendency of males to void at seemingly inappropriate times might be similar to the action of dogs in spreading their scent through urinating on posts and other prominent objects.

Interactions between neighboring males.—Encounters between neighboring males are sometimes brought about when one resident male pursues a troop into the territory of a second, which then attacks the first male rather than the troop. Other encounters result when an alarmed band flees into an alien territory. But usually hostilities grow out of the fact that neighboring bands gradually draw together as they graze at a favored site. At least on the better grazing sites where encounters between bands occur daily, the line that must be crossed to elicit attack is well-defined. There seems to be no neutral zone between territories, for by watching the drift of a band toward a certain boulder or other landmark that I knew lay on the mutual boundary, I could often predict with fair accuracy when the adjacent family male would come to defend his boundary.

Characteristically a family male interposes himself between his females and an intruder. When neighboring bands graze close to each other on opposite sides of their mutual territorial boundary, the family males usually stand a short distance toward the opposite band from their females, and the males are the closest members of the two groups. Whenever members of one band reach the line separating the two territories, the male of the opposite band drives them back by display, feints, or attack.

An example of the frequency and kinds of en-

counters that occur between two bands grazing near their mutual territorial boundary is the following synopsis of actions observed during a period of 3.5 hrs one morning (July 20, 1951) at Aricoma.

8:15 Bands A (5 members) and B (4 members) 100 yds apart, except male A halfway between.
8:30 Females of A join their male.
8:35 Male B stood 20 yds from band A, which then retreated 25 yds.
8:50 Band A to 20 yds from male B.
8:55 Male B stood staring at band A, which then retired 15 yds.
9:15 All save one prone; males 30 yds apart.
9:55 All standing. Male B walked 10 yds toward band A, which retreated.
10:00 Male B 20 yds from nearest member band A. All grazed peaceably. Male B ran several steps toward band A. Male A, displaying, followed male B as he retreated.
10:05 Male B ran 10 steps toward band A, then retreated. Again male B walked 30 yds toward band A, which retreated. Male A ran at male B, which retreated.
10:15 Bands grazed 100 yds apart, A having moved away.
10:25 Male A ran to point 30 yds from male B. Males stood in display, then grazed.
10:35 Male A ran 20 yds toward nearest member (female) B; she fled. Male B ran 5 yds toward male A.
11:15 Band A moved toward B. Bands grazed 30 yds apart. Male B ran few steps toward band A, which retreated. Male A chased back male B.
11:20 Male B stood 5 yds from band A, made short feint, retired 10 yds. Another feint by male B. Nearest members band A retired few steps.
11:25 Male B walked away to point 50 yds distant from band A.
12:00 No more encounters by this time.

The mutual boundary between bands A and B extended through two choice grazing areas, one of which was favored in the morning, the other, 300 yds downslope from the first, favored in the afternoon. The movement of the bands from the upper to the lower site often brought about boundary violations and hostilities. For example, one day as the members of band A started for the lower forage area the male of band B, a quarter mile distant, started to run toward them. As the hostile male neared, the rear member of A, a female, darted ahead to join her group. Band A soon halted at a customary site in a small valley and commenced to graze. The male of band B approached band A but stopped atop a ridge 50 yds distant. This ridge seemed to be at the territorial boundary. The females of band B joined their male. No hostilities occurred between the bands until band A moved a short distance out of the valley and onto a flat. Then the male of band B chased band A back into the valley. Some time later, in the course of grazing, band A neared a certain large boulder, the site of many previous encounters with band B. When the male of band B came running, band A retreated. Within the next hour and a half, there were 4 more encounters at the same site.

It was found that the male of band B attacked band A much more frequently, and starting from greater distance, than the male of A attacked band B. This fact suggests, as earlier noted for resident males attacking troops, that there is much variation in the belligerence of males in defending their territories. Nevertheless, in encounters between neighboring bands it might be that one tends to cross the boundary, perhaps to reach greener grass, more often than the other. The militance of the male does not seem to be affected by the possession of a family, for some solitary males are as vigorous in territorial defense as any males having large families. Nevertheless, the two least pugnacious resident males that I discovered were solitary.

In attacking a neighboring male near the mutual territorial boundary, a family male may run a short distance into the neighbor's territory. As a male is normally invincible in his own territory, the second male may then chase the first back across the line, and yet again the chase may reverse. Thus a "pendulum" action (Tinbergen, 1952:12) results, the two males going first one way, then the other, as the roles of pursuer and pursued are exchanged. When 3 territories adjoin on a favored area of pasturage, all 3 family males are sometimes involved in attacks and counter-attacks. Here are two observations of strong pendulum action between band males:

In one observation, a large band walked across the boundary that separated it from the territory of a second smaller band, the male of the second band ran toward the intruders from a point 300 yds distant, and the first group fled back into its own territory. Then the attacker halted, the fleeing band stopped, and its male turned about and chased the assailant. Finally the two males stood in display 10 yds apart. Soon the last pursuer, the male of the first band, walked toward a dung pile and the second male chased him a short distance. Three minutes after the start of the action both males had rejoined their families. In the second observation too, the male of one band galloped a long distance to chase a larger band at his territorial boundary. When the male of the second group counter-attacked, the first male fled 50 yds back into his own territory, jumped up onto a dung pile, kicked up his heels, and then dashed back toward the other male. But the latter again reversed the action and chased the first male back. The entire action changed the position of the trespassing band less than 10 yds.

Fighting between band males.—Vicuñas in the wild rarely fight, in the sense of struggling physically with the object of inflicting injury. True fighting is similar to play-fighting in method but it is ferocious and it typically includes hard biting. A bite would be rather harmless were it not for the three pairs of

long backward curving caniniform teeth (I 3/, C 1/1). These teeth seem to be useful only for fighting, and principally for biting the neck or other part of small diameter. Judged by examination of skulls, these teeth are the last to be replaced in lamoids. In juvenile and yearling vicuñas, the ones that habitually engage in play-fights, the caniniform teeth do not protrude through the gums, but in adults these pointed teeth extend from the bone of the jaw a distance of as much as 6 mm in females and 12 mm in males.

At Aricoma I saw the final moments of a fight between the males of bands A and B. One afternoon in July band B started walking downhill toward the lower flats of its territory and band A soon followed. When the latter band had walked only 100 yds, the male of B turned back up the slope in aggressive manner and band A retreated uphill. About 2 hours later, shortly after sunset, loud grunts and shrieks attracted my attention to a fight between the 2 males. They fought violently at a point near the boundary between the lower parts of their territories. Several times one male bit the dorsal side of the neck of the other. Finally band A retired up the slope, its male making an occasional feint back toward band B which remained below. For many minutes after the battle the lips of the male of band B hung agape as if with panting.

At Huaylarco I watched another short fight between adult males. A large displaced band and its male were being driven out of a territory by the resident male when a third male, possibly the resident of a nearby territory, joined in the pursuit and uttered shrill cries. This male attacked the retreating band and viciously fought its leader for a quarter of a minute. The fight included much tripping with head and wrestling with necks as well as biting of necks. Finally the third male was chased away. The other two stood calmly a number of yds apart, the male of the displaced band with a large tuft of vicuña hair in his gaping jaws.

On occasions an adult male bites another without fighting. In one observation, a family male broke off his pursuit of a troop in order to attack an adult male that approached his females. Although the two scarcely touched, the intruder bit his attacker quickly and secured a mouthful of wool. Before withdrawing the males displayed 5 yds apart, uttering low cries, one then the other spitting.

Tolerance between band males.—Under some conditions a resident male may tolerate an alien band on his territory, at least if the transgressing band is a neighboring one. For example, during one day at Aricoma the vicuñas were frequently disturbed by livestock. At one time a band of 5 members came over a low ridge and entered the territory of neighboring band B. The resident male attacked the intruders, but they eluded him and joined his females. After a confused chase involving many vicuñas the groups drew apart, but both bands remained in the territory of B. Half an hour later the 5 invaders ran close to the resident male and he chased them a short distance. But during the next hour he did not again molest them. In this observation, the male of B may have been relatively tolerant of his neighbors because he had suffered repeated disturbance from alien vicuñas during the day. On another occasion, the same male allowed the 5 members of neighboring band A to remain on his territory for half an hour. In returning toward its territory after a long absence, band A walked across the territory of B and loitered there, some of its members lying down. The male of B displayed near at hand, but he did not attack band A until it walked close to his females.

One observation suggested that a male which was unable to defend his territory might be driven out of it by other adult males, as if his lack of aggressive behavior invited attack. Two days after a sick male lost his family, I saw him grazing on his territory. Fifty yds away a second male defecated, then ran toward the sick one, which retreated 20 yds. A third male, from an adjoining territory, chased the sick one up a slope and the second male joined in the chase. From time to time both healthy males stood in display close to the sick one. Finally he ran back downhill into his territory, pursued by his neighbor. The latter soon returned to his females, but the second male followed the sick one as it ascended another slope, apparently leaving the territory he had defended a few days earlier.

The fact that a resident male greets some invading adult males with less belligerence than others may be due in part to the kind or quantity of sign stimuli presented by the invader. In one observation, an injured male that had lost his band and wandered from his territory entered the territory of another male. Although the latter male had attacked several transgressors, he did not attack the sick one, presumably because it did not display male aggressiveness. Other cases of differing hostility between males might be due to the fact that individuals are recognized and then treated in the light of past experience.

Reactions between resident males and displaced bands.—An alarmed band may flee to a point far beyond the limits of its territory. In returning to its territory this displaced band crosses the territories of various resident males, which attack the aliens. But between two displaced bands within the territory of a third there is little hostility, even though the 2 bands are separated by a distance of only 10 yds. Here is an example of the action between a resident male and displaced bands. One day I noted 3 alien bands, of 7, 6, and 4 members, grazing a short distance apart on the territory of a solitary male. After some time the resident male attacked the 7 and chased them 50 yds. Soon the male of the 6, tail up, approached the lone male and stood near him. The latter gave chase and pursued the alien and his family up a slope. Next the resident male chased the band of 4, then the 7, and again the 4. The displaced bands retreated up an increasingly barren hillside, and the solitary male followed to a point 20 yds above the limit of grass. In another observation, I saw a band of 15 vicuñas driven from 4 territories,

one soon after the other, by the resident males. These territories were located in a line along one side of a stream. In the course of half an hour the pursuits moved the displaced band a distance of 1,000 yds.

As in other relations toward intruders, resident males differ in their belligerence toward displaced bands. For example, once a displaced band of 7 members crossed the edge of the teritory of a band of 6 and entered the adjacent territory of a band of 5. The resident male of this last band ran 300 yds to attack the invading 7. These fled back into the territory of the 6 and stopped 150 yds distant from that band. Although the resident male ran to a point near the aliens and displayed, he did not attack but soon returned to his family. In the course of grazing the displaced band drew nearer to the residents until it reached a point only 100 yds away. Then the resident male displayed near the intruders, which retreated. Several times during the next hour the 7 reached a point about 100 yds from the resident male, but he took no apparent interest in them. Yet, as soon as the 7 again entered the territory of the 5 vicuñas the male of that group attacked. Evidently the male of the band of 5 was much more belligerent toward the displaced group than the male of the band of 6, for the latter allowed the aliens to graze on his territory for more than an hour.

Observations suggested that the resident male is more aggressiye toward a displaced band from a distant territory than toward a transgressing band from a neighboring territory. It appeared that the dominance of the resident male is not entirely conceded by an alien male from a distance. This lack of submissiveness, as contrasted to the ready submission of trespassing neighboring males, is illustrated by the following observations. When a displaced band retreats under attack its male usually runs from side to side behind his females, keeping between them and the attacking resident male. If the pursuer presses close the alien male may kick at his head. While one band retreated its male, in aggressive attitude, ran back toward the pursuing male and kept him about 20 yds behind the retreating females as they walked slowly away. And on another occasion, under attack of the resident male a displaced band retreated slowly, its male occasionally kicking back at his pursuer. Soon the departing band crossed a stream which lay at the territorial boundary. The family of the resident male started to follow, but the alien male turned and chased him back. Then the displaced band grazed just across the stream from the resident group, and when members of the band across the stream drew near, the alien male dashed a few yards toward them and they fled deeper into their territory.

Hostility of resident males toward alien band females.—A territorial male acts aggressively toward the females of neighboring bands. If these females approach his territorial boundary, he moves toward them or displays and the females retreat. And if an entire band invades his territory, the resident male may chase the females as vigorously as he chases the intruding male. Even a single female of a band is attacked if she wanders into an adjoining territory.

Here are two observations which illustrate aggression by resident males toward neighboring band females: In the first observation, the four females of one territory walked away from their male and toward a second territory, 200 yds distant. The male of the second territory came toward the females, and when he reached a point 75 yds distant, they retreated. Soon a female of the second band ran to a point 20 yds from the male of the first, which was lying down. He rose and chased her vigorously. In the second example, two bands were grazing near their mutual territorial boundary when the male of one band chased a female of the other. At this, the male of the second band drove the first male back. The groups grazed several yds apart for a few minutes, then again the first male chased a female of the second. He pursued her around in a circle three times, then on a straight course for about 300 yds.

While a male is far from his family, neighboring males may attack his females. In one observation, the male of a large band moved far away from his family in chasing another vicuña. A female of the deserted family ran downhill toward a second band. The male of this band attacked the female, then continued on uphill and chased the other females of her group. Another time, under similar circumstances, a male attacked the deserted family of a neighboring band and chased one mother, then another, out of the group and back again. Although these observations were made in the mating season, similar attacks were seen late in the year when females probably would have no sexual attraction for males.

In both of the foregoing examples of an alien family male chasing females on their territory, the absent male quickly returned and drove off the intruder. Evidently the factor that normally prevents the family from being attacked by other males is the presence of the band male. On occasions an attack on the females is instigated by the departure of their guardian. One afternoon bands A and B grazed approximately 100 yds apart. About every half hour the male of B made a sortie toward band A. Finally he galloped off toward a single vicuña, 200 yds away. As soon as this male departed the male of band A ran toward the females of B, and they fled.

When an attacking male runs toward a group of females they usually stand and face him, like any other aproaching vicuña, before they turn and flee. They may start away when a male 100 yds distant merely runs a few steps toward them. Frequently at the start of an encounter between their males, families a short distance apart run several steps away from the belligerents. Band females were never observed to show hostility toward a male that attacked them.

Tolerance of resident males toward unattached females.—One or two females, with or without juveniles, far separated from their band and territory (if any), tend to join groups of band females. Gener-

ally the male of a band allows the alien females to join and, after initial recognition, shows no hostility toward them. For example, 2 single adult females approached a well-known resident band from different directions. The male of the band ran toward one female, stopped, then ran toward the other, not approaching either to a point less than 10 yds distant. At first the females grazed 50 yds from the band but soon they moved closer. After a time the male ran to meet still another approaching female. Both she and the male ran to the group when an automobile neared. Half an hour later the 3 new females were still with the band.

On a few occasions at various seasons of the year, I observed mild hostility of a resident male toward a female and juvenile that tried to join his family. In one instance (April, in the mating season), the resident male of a large band drove away a female with a small juvenile when she approached his family. He chased her way from the band, then back and forth a distance of about 100 yds, often pursuing so closely that he seemed to touch her with his chest. After the chase the female and juvenile grazed about 100 yds distant from the band for a quarter of an hour. When the two finally started away the male chased the female as far as his territorial boundary, and the youngster followed.

In another observation (February), I saw an adult female, closely accompanied by a female yearling, cross a stream and run to a resident band of 12 members. The band male followed the joiners a short distance. After many minutes with the band and some show of hostility by the band females, the newcomers ran 150 yds away. When they again drew near the male ran a short distance toward them, and they retreated 100 yds. Again the two approached. The male dashed at them and the intruders fled across a stream. Half an hour after the start of this action the pair returned across the stream, ran past the male, which was 100 yds from his family, and joined his females. The male ran several yards toward this group, but he remained at a distance. The two stayed with the band for a quarter of an hour, then departed and joined another band. The male of this second band continued to graze and seemed to take no interest in the newcomers. An hour later, while the male of the first band was far off from his family, the two females rejoined it. When the male returned, he again chased them away. Pearson (1951:168) also records an observation (September) of a female and a juvenile being driven away from groups that they attempted to join.

On a few other occasions, I saw a resident male drive off a single female that joined his family. In one instance, a single immature female gradually moved closer to band A until she grazed close to one of the band females. Ten minutes later the resident male chased the newcomer away. In another observation, a strange female approached a band three times, and each time she was driven away by the male; then she departed. The fact that unattached females which try to join bands are often met with hostility apparently keeps these females on the move until they encounter a male which will accept them into his band.

Within two bands, I noted hostility toward a newly joined female by a resident male that had been without a family. One male (W. 139.4) was injured, lost his family, and left his territory. Two weeks later (early April) he was back in his territory. He was thin and his coat was scraggly. Near him lay an adult female. He blew at her and she rose. She started to defecate but walked away at the approach of the male. The two grazed several yards apart, the male following the female back and forth over a distance of about 100 yds. The following day the male was once seen to chase the female, but in occasional observations during the next 3 weeks no animosity was noted. The other observation was made a few days after 3 yearlings joined a lone male (W. 138.2) which had lost his family. When the smallest yearling gamboled about, the male chased it several times as if trying to drive it away. Once he chased the other 2 females, but all 3 remained in the band.

Evidently the resident male treats certain unattached females with about the same hostility as he treats the established females of neighboring bands. Usually, however, the male takes little interest in females that join his band. Band females, on the other hand, are hostile toward joining females.

Hostility of resident females toward unattached females.—The females of a band form an incompletely closed society into which new members are not readily admitted. In contrast to the usual actions of the band male, band females show curiosity and hostility toward a joining female. In one observation, when an adult and a yearling female joined a large band the resident male merely followed them a few steps. But four band females, necks craned, slowly walked up to the new adult and nosed the base of her tail. One female stood several feet in front of the newcomers and spat into the air. Two females in turn, tails high, chased the aliens a few steps. The joining couple grazed several yards from the band and soon ran off, unpursued. Some time later the two females again joined the band. The male remained 100 yds distant, but a band female chased one of the newcomers and bumped her with chest and forelegs. After a time the strangers departed and joined another band. The females of this band inspected the two with outstretched muzzles before permitting them to graze with them. An hour later, when the two females returned to the first band, the band females drew together, and one pursued the strangers a few yards.

At Aricoma I observed many of the reactions between the established females of a band and an adult female that joined them. One afternoon in July a strange female joined the family of band A, an adult and three immature females. The stranger ran toward the group, stopped 30 yds away, ran closer, and stood tensely. A female of the band ap-

proached the newcomer and held its extended muzzle within a few feet of her. The latter faced away with head high, ears back, and tail arched. Soon both females relaxed and grazed. The stranger ran several steps away when an immature female ran toward her. She stood, apparently spitting into the air, as the immature inspected her from the rear. For a quarter of an hour she grazed without being molested, but then an immature chased her for several yards and mounted her back. At this she spat and ran out from under the smaller one.

Early the next morning I saw the new female lying down with the established members of the band as if one of them, only 10 yds from her nearest neighbor. A few minutes after all had risen, one female chased the new one a short distance. Twice the newcomer started to defecate but, after letting a few pellets fall, she walked quickly away as if alarmed by those nearby. When other females approached her from the rear, or when she approached them, she held her tail out and head high. Most of that day the new member grazed 30-100 yds from the other females. The following morning, shortly after the new female arose an immature chased her and she fled. For more than 2 weeks she remained with the band, but further hostility toward her was not apparent. It seemed that the joining female was initially treated as a subordinate by all the established band females, including some immatures.

In summary, the usual relationship between a resident band and unattached females is as follows. The females are attracted to bands. Usually the resident male allows them to join, although he may not. Established females of the band are hostile toward a joining one, but if the alien female does not leave the group, hostility toward her ceases within a few days. Similar initial unfriendliness by members of a closed group toward aliens that join occurs in other kinds of vertebrates (Dice 1952:276).

Association of juveniles from different bands.—Young juveniles often join the young of neighboring bands for play. One mixed group included 7 infants 3-6 weeks of age. When two bands grazed on opposite sides of their mutual boundary, at distances 20-100 yds apart, a composite group of 6 small young remained for a time with one family then the other. The 4 infants of a band of 10 members sometimes played with the 4 of a neighboring band of 13 members and at other times with the 2 young of a band of 9 members. In one observation, a mixed group of 6 juveniles was playing near a road when an approaching truck alarmed them. They all ran to their proper bands, save one youngster which ran to the wrong group. Five minutes later it returned to the proper band. In another observation, a displaced band which had 1 juvenile was joined by 2 juveniles from the resident band. The 2 stayed with the alien band until they were 100 yds distant from the resident group; then they returned to it. After juveniles pass the age of 6 months they tend less and less to join the young of other bands.

Tolerance of adults for alien juveniles.—When playing juveniles from one band run close to the adults of another band, these adults usually take no more notice of the alien young than of their own. In one instance, when a juvenile a few weeks old joined the young of another band some of the resident females nosed its back, head, and neck. The infant, tail up, shied away from these nuzzlings and, within a few minutes, the females lost interest. Soon afterward this infant and 7 others, 3 from an alien band, played together among the resident females. From time to time a female took a few steps toward one of the youngsters as it ran close to her.

When young more than 6 months of age approach the adult females of another band the females may chase them. In one observation, an old juvenile joined 3 adult females while their male was absent. The females chased the juvenile mildly at first and then left it alone for several minutes, but finally one female chased the youngster away. In another observation, I saw a juvenile about 8 months old walk to a point several yards from a neighboring band. A female of that band cautiously walked up to the youngster as if to inspect it, but she hastily retreated when the young one raised its tail high and spit. In general, an old juvenile that strays from its home territory is treated by the adult females of other bands if it were an unattached adult female.

An old juvenile is also treated like an adult female by the male of an alien band. In the event that a youngster steps out of its territory it may be chased by a neighboring resident male. In one observation, a large band, which included 5 old juveniles, grazed close to a band on the opposite side of the territorial boundary. Whenever some juveniles of the large band reached the boundary the male of the adjacent band charged at them. He nearly overtook one of the youngsters before it reached its own family. Again, 2 large bands were grazing 20 yds apart when the 2 old juveniles of one group joined the young of a second. The male of the second band chased one juvenile back and the other followed. Not long afterward, 2 juveniles of the first band again joined the second. The resident male walked, then ran, toward them; they fled to their family.

TERRITORIAL BOUNDARIES

Size of territories.—The boundaries of 18 territories at Huaylarco were approximately determined (Fig. 18 and 19). The areas of these territories range from 20 to 115 acres in horizontal plane, the median being 32 acres. If allowance were made for slope the areas of the smaller territories would be as much as one-quarter greater than indicated, but the areas of the larger would be little changed. For convenience, my studies were made where population densities were high and the size of territories small. In rather barren parts of the vicuña range territories might be huge, more than 250 acres in area.

Evidently forage density strongly influences the size of vicuña territories. At Huaylarco the larger territories were located where vegetation was sparse

and coarse, the smaller territories where forage was relatively abundant and succulent. This difference in territorial size is obvious from comparison of the map of the more barren territories, on the western part of the study area (Fig. 19), with the map of the more vegetated territories, on the eastern part of the study area (Fig. 18). Abundant forage permits a band to find enough to eat on a small area.

It seems probable that the size of territories corresponds approximately to the area necessary to supply forage for a band of vicuñas. In the Huaylarco study area, just before the young were born, for the average territory of 32 acres the average band size was 5.3 vicuñas, or 1 vicuña per 6 acres. This rate of stocking is judged to be near the carrying capacity of the bands and of encounters. Using the plotted data, of the best range.

Large territories tend to have larger bands than small territories. At Huaylarco during the last half of February, of nine bands that included more than the median number of members (6), two-thirds occupied territories that were larger than the median area. Extremely large bands (18 to 26 members) were seen only on territories 60 acres or more in area (S. 133.0, N. 134.5, S. 133.2). Why should large territories have large bands? For one thing, the females of a band on a large territory seldom approach the perimeter so they rarely have opportunity to leave. Further, disturbance is infrequent on a large territory because forage is sparse and not especially attractive to other vicuñas or livestock.

On the other hand, moderately large bands may inhabit small territories. Bands containing 11 adults and 4-5 young occupied territories of only 20 acres (S. 139.0) or 30 acres (E. 137.5) for periods of a few weeks. Rarely, however, do small bands inhabit large territories. At Huaylarco, of the territories larger than 50 acres only 1 out of 6 held a band of less than the median number of members. In this exception a single male occupied a territory of 115 acres (N. 133.5) of apparently low forage value. Approximately two-thirds of the territories smaller than median size were occupied by bands having 5 members or less.

Shape of territories.—In areas where forage and topography are fairly uniform, territories tend to be circular in outline (Fig. 18, W. 139.4; Fig. 19, S. 133.2, N. 133.5). The presumed reason for this shape is that a circular territory has the least perimeter, which must be defended, for a given area of forage. Many territories at Huaylarco were elongated in shape because they were situated in a narrow, grassy, valley bottom bordered by rocky ridges. A few portions of territories interlocked (Fig. 18, area east of km 138.0). Some observations suggested that where favored grazing sites occur as more or less isolated patches in surrounding barren areas, a territory might be dumbbell-shaped, or divided into separate parts with an undefended zone between them. In these territories one part would be favored and the second used on occasions, such as when there was disturbance on the first.

Geography of territories.—Nearly all of the territories studied included moderately steep slopes which were used for retreat or for resting at night. At Huaylarco those bands that lived principally on low rolling hills or pampas (Fig. 19, bands S. 133.0, N. 133.5, S. 133.2) either had territories bounded by ascending slopes or they could reach slopes by running less than half a mile out of their territories. Within no greater distance of all the groups of vicuñas that I saw there were some slopes, such as those bordering stream-beds.

The foot of a slope is a choice site for grazing not only because an uphill retreat is close at hand, but because succulent food is relatively plentiful there. Soil is generally deeper and moister at the foot of a slope than farther uphill. Water, too, is commonly found on the surface near the foot of slopes. All of the territories that I studied included some water.

Late in the year the puna becomes increasingly arid until the start of the rainy season causes a rapid increase of water. Water was apparently the major factor causing one territorial change observed at Huaylarco. In November and early December, when the land was dry, one band occupied a territory (Fig 19, dotted outline) that reached to the shores of a lake. Soon after rains commenced the lake rose and covered about 50 acres of the southeast end of the territory, and a previously dry stream, situated a short distance beyond the opposite end of the territory, commenced to flow. The band, apparently crowded out of much of its old territory by the rising lake, moved northwest and occupied a much smaller area than before (Fig. 19, S. 133.0, broken line). The new territory slightly overlapped the old and included a loop of the stream. In March the male of this band was injured and his family dispersed. The stream dried up a short time later. This territory was not reoccupied by the time, several weeks later, that my studies ceased. Probably the area of the stream-bed became unsuitable for a vicuña band when the water disappeared.

Segments of the boundaries of vicuña territories often coincide with geographic features, such as roads, ridges, or streams. For example (Fig. 18 and 19), a road separated the territories of bands E. 139.0 and W. 139.4, and parts of the territories of bands S.133.2 and N. 133.5. Ridgetops formed barren peninsulas of unclaimed ground between some territories, such as E. 138.2 and E. 138.4, and bounded many territories on one side. Upslope boundaries that lay at the foot of rock slides or barren slopes rarely needed to be defended. A stream separated much of territory S. 132.8 from S. 133.2, and E. 138.2 from W. 138.2. It is not surprising that streams correspond with some boundaries, for a stream-bed and water break the continuity of forage and hinder crossing. Further, boundaries at streams are strongly contested, for the adjacent ground commonly bears lush and abundant forage.

Relations of band males to territorial boundaries.—There may be no physiographic or vegetational change at sites where the territorial boundary passes through

optimal forage. At these sites the boundary is apparently delineated by many encounters between neighboring family males. Such segments of boundaries are tested daily, or several times a day, while other segments may not be tested for periods of many days. Although the territories that seem most choice are not necessarily occupied by the most aggressive males, the exact location of a mutual boundary seems to depend upon the relative belligerence of neighboring males over a period of time. If the male of a territory were replaced by another, I suspect that there would soon be a change in the territorial boundaries, especially those unmarked by physiographic differences.

Once established, the territorial boundary is recognized by the male on each side of it. The line does not change position readily, even though it is not defended by one male. In one observation, although the male of a band (W. 138.2) was sick and unable to defend his territory, the male of the adjacent territory (E. 138.2) defended it only to the usual boundary, 200 yds southeast of a stream (Fig. 18, dotted boundary). But 4 days later the healthy male carried his defense clear to the bank of the stream. After a few days the first male was able to resume defensive action, but now he regarded the stream as his southeastern boundary. He did not cross the stream into the former part of his territory even though a troop of males, a target which normally invited attack, stood on the opposite bank. Thenceforth the stream marked the mutual boundary between the bands (Fig. 18, broken line between E. 138.2 and W. 138.2).

On another occasion when a male (W. 139.4) was injured, he remained on his territory for a few days. The neighboring male, which had fallen heir to the family lost by the first, recognized the same mutual boundary as before even though the first male did not defend it. The injured male finally left his territory and remained away for several days, but when he returned the mutual boundary was the same as before. Evidently an undefended territory may not be occupied immediately by neighboring males.

Territorial boundaries may be stable for long periods of time. Most of them remain essentially the same throughout the year. In the territories of 2 bands at Aricoma, no major change occurred during a period of 5 months. For each of the bands studied at Huaylarco, I kept a chart of the observed locations of the bands and of encounters. Using the plotted data, at the end of each month I made a map of the approximate boundary of each territory. Over a period of six months only two large changes in boundaries were detected.

In one boundary change, the territory of a band (S. 133.0) moved about 600 yds when a lake covered one end of the territory and a stream commenced to flow in the new area. In the other change, a male lost one sector of his territory because he was injured. This male held a certain territory (Fig. 18, W. 138.2 including dotted outline) until mid-January. Then one day I discovered that he was sick, barely able to stand. Within a period of 4 days, one neighboring male (E. 138.2) enlarged his territory to include about 2 acres of the sick one's former area. A second segment of the sick one's old territory was soon annexed by a single male from another adjacent territory (W. 138.6). The new boundaries were observed after the sick male recovered.

The fact that a male defends a territory even when he has no family indicates that it is the area, not the family, which is defended. Perhaps the situation is similar to that in some birds where the male defends the future nesting territory before the arrival of the female. Furthermore, a change in the size of the vicuña family causes no change in the territory. In one clear observation, the females of a band (W. 139.4) deserted their injured male and joined an adjacent male, thus increasing his family from 1 to 10 members. But in spite of the great change in the size of his family, this male (W. 139.0) continued to defend the same boundaries as before.

Relation of the family band to the territory.— Although band females are hostile toward alien females, they do not take part in defending the territorial boundary. And even though the male does not actively prevent the females from leaving his territory, they stay in it. Apparently gregariousness and mutual tolerance among band females serve to keep them together, and their tendency to follow the male normally keeps them in his territory. Females are restrained from leaving some territories by the barrenness of the adjacent ground, but the hostility of neighboring males also acts to keep them from leaving. If a female wanders to the boundary of the territory, she is usually driven back in by the male of the adjacent territory. This hostility of territorial males also would appear to speed the return of a displaced band to its territory. Away from its home ground, a displaced band can long occupy only unclaimed ground, which is generally poor in forage. The only good grazing site where a band can feed in peace is its own territory.

In spite of these factors, it is presumably the familiarity of home ground that is the principal factor which keeps a band in its territory. This seems evident from the fact that if a band of vicuñas is driven from its territory, and even if the animals are then separated from one another, they soon return to it. At Aricoma, 2 bands were driven from their territories by livestock and their herders almost every day for a period of two weeks. Yet, on subsequent days when the stock was absent the vicuñas occupied the same territories as before.

A band of vicuñas does not use all parts of its territory equally. Parts of large territories may not be visited for periods of days, and on small territories only a fraction of the area may be traveled during one day. The favored sectors for foraging are the damper sites where plants are lush, and for night-resting a certain slope is favored. Mid-morning and late afternoon headquarters are commonly at different sites. This difference seems to be correlated with

the fact that the drive of hunger is greatest in late afternoon. When hungry, vicuñas may seek the sites with the best forage but which are subject to disturbance or are far from retreats.

THE FUNCTION OF TERRITORY IN THE VICUÑA

Our understanding of territoriality in animals has been developed primarily through studies of birds. One of the foremost students of this subject is Margaret Nice, who states (1941:441) that "the theory of territory in bird life is briefly this: that pairs are spaced through the pugnacity of males towards others of their own species and sex; that song and display of plumage and other signals are a warning to other males and an invitation to a female; that males fight primarily for territory and not over mates; that the owner of a territory is nearly invincible in his territory; and finally that birds which fail to obtain territory form a reserve supply from which replacements come in case of death of owners of territories."

With some modifications these statements apply to territory in the vicuña. The spaced unit in vicuñas is not a pair but a family band. The display of the male warns other males, as in birds, though it is not clearly an invitation to females. A territorial male vicuña is pugnacious toward other males. He defends his territory, not his females. He is rarely opposed, much less defeated, by another male in his own territory. Troop males, without territory, form a reserve supply of males.

Nice *(op. cit.*: 457) recognizes six types of territory, depending upon the kind of activities conducted on the defended area. Territory in the vicuña is of the most inclusive type, Type A, the classical "true territory" in which mating, birth and feeding of young occur. As in some birds, the vicuña territory is held all year, not only during the breeding season. This type of territory has apparently not previously been recognized in mammals.

Several examples of supposed territory in mammals are discussed by Nice (1941:467) and by Dice (1952:-241-242). Burt (1943) regards the lack of overlap in portions of the home ranges of neighboring mice to be an indication that part of the home range is defended, and is thus a territory. Moreover, he considers that energetic defense of a supply of food by a squirrel, which pursued invaders to fairly constant limits, is an outstanding example of territorial behavior in mammals. It is debatable whether these examples are valid, for intolerant behavior in mammals is easily confused with territorial behavior. To demonstrate territoriality in the strict sense it should be shown that the defended site has fixed limits on the ground over a considerable period of time. Defense of a breeding ground by the adult male fur seal appears to be a clear example of territoriality in mammals. But in contrast to the territory of a vicuña, the seal territory is defended only during several weeks of the year and it is not a feeding ground.

In other species of mammals social groups may defend an area. Carpenter (1934) found that clans of howling monkeys tended to occupy definite and limited areas, but with some overlapping. When 2 clans draw near to each other a vocal battle ensues between them, the group males coming closest and being most active in roaring. Then the opposing clans retreat. More recently King (1955) discovered that social groups within colonies of black-tailed prairie dogs defend a discrete area against members of other groups. Defense is principally by bluffing attack without actual contact. Females and young may participate in defense, but the dominant male of the group is most active in guarding the area. In all probability, future studies of mammals will disclose many examples of different kinds and degrees of territorial behavior. Analysis of these examples will add greatly to our understanding of the evolution and function of territoriality in all animals.

The assumed advantages of territory are many. How does territorial behavior benefit the vicuña? The protection from other vicuñas of a feeding area for the family band is an advantage, for even in the absence of disturbance the eating of sufficient quantities of food requires several hours a day. And it seems evident that the spacing of groups prevents the overgrazing of choice sites, with consequent lowering of the carrying capacity of the range. Territorial behavior also appears to reduce strife between aggressive male vicuñas, for the frequency of encounters between them is reduced by the acquaintance of neighboring males with the boundaries of one another, and encounters consist not of actual fighting but of formalized display. It is suggested by Darling (1952) that such apparently aggressive display in mammals and birds provides the males with social stimulation which is necessary for high success in reproductive activities, and that territory increases opportunity for this stimulation.

On the other hand, some of the assumed advantages of territoriality might be of little benefit to the vicuña. The fact that territory seems to protect females and young from alien males might be of no advantage, for alien males are rarely aggressive toward these. Protection of the family against carnivores and livestock would seem to be of much greater value to the vicuña band, but little evidence of defense against these was discovered. And although territorial behavior guards the feeding area from neighboring bands, it is much less effective in protecting it from invasion by male troops, which are larger than bands and are relatively insensible to aggression by territorial males. In all, reduction of strife, protection of a feeding area, and prevention of overgrazing are the most probable advantages of territorial behavior in the vicuña.

RELATIONS WITH OTHER VERTEBRATES

PREDATORS

The domestic dog, Andean fox *(Dusicyon culpaeus)*, condor *(Vultur gryphus)*, puma *(Felis concolor)*, and wildcats *(Felis colocolo* and *jacobita)* are potential enemies of the vicuña. With the exception of the

dog, these predators have doubtless influenced the evolution of defensive behavior in the vicuña during past ages. But today it appears that the behavior of greatest defensive value is to flee when a man or dog approaches.

Dogs are the principal carnivorous enemies of vicuñas. This I judge from many observations of dogs chasing vicuñas, and from the accounts of local residents. Capture of infant vicuñas by hunters using dogs is generally said to be common practice, although I did not witness it. The domestic herd at Calacala was started with about 30 young vicuñas caught with the aid of dogs. During my stay at that ranch a young vicuña was killed by two house dogs, which were well-kept setters. In comparison with these, the dogs of native herdsmen are vicious, hungry, and wide-ranging. Wherever there are Indians there are savage dogs which chase vicuñas.

Most of the Indian dogs are black, shaggy with shed hair, and of heavy build like a setter or large spaniel. Perhaps because of starvation, these dogs are neither cunning, agile, nor swift. Even yearling vicuñas outrun them. One dog gave up pursuit of a group of vicuñas after it stumbled and fell; others gave up after being outdistanced hundreds of yards. In some observations, a dog pursued one vicuña for a long distance and then shifted his pursuit to a fresh one—hardly good tactics. It is fortunate for vicuñas that these dogs do not hunt in packs. I did not see more than two dogs hunting together, but even two should have little difficulty in killing an infant vicuña.

An adult vicuña, however, could probably well defend itself against a dog. On one occasion, a black setter accompanied me on a walk through a pasture where many domestic vicuñas grazed. Several of them approached to a distance of about 30 yds from the dog and stared. Finally two immature vicuñas vigorously chased the dog and it fled. Later, in a corral, this dog was viciously pursued by a vicuña-alpaca hybrid, which struck at the dog with its forefeet.

Aside from the fact that dogs may wound or kill vicuñas, chasing has other harmful effects on them. Energy hard-won is expended in flight. Galloping over rough ground may cause leg injuries. Some bands are driven onto barren slopes where forage is scanty. Others flee into alien territories where interband conflicts arise. Mating may be interrupted. Pregnant females, new mothers, and tiny young are forced to extreme exertion. In short, when dogs chase vicuñas energy is wasted, crippling increased, feeding efficiency lessened, reproductive success diminished, and the advantages of territorial separation are lost.

The Andean fox, the ecological equivalent of our coyote, is common in the highlands. In contrast to the dog, this fox seems to take no interest in vicuñas, at least by day. In one observation, a fox walked through a band of 6 vicuñas 3 times during a period of 1.5 hrs. It urinated and even lay down while vicuñas were following it. Possibly the relation between vicuña and fox is not always harmless, especially at night or when tiny young are present. Sr. Paredes blamed foxes for the low reproductive success of his ranch vicuñas, but he cited to me only evidence of foxes feeding on vicuña carcasses, not observations of actual killing.

Nor did the superintendent of the Granja Modelo at La Raya cite direct evidence when he told me that many vicuñas had been killed there, within fenced pastures, by pumas. There large cats are uncommon in the vicuña range, but both Pearson and I have found fresh puma tracks in areas where there were vicuñas. It would seem that, within its range, the vicuña would be the principal natural prey of the puma. Too little is known of the long-tailed wildcats of the highlands to appraise their effects as predators.

The vicuña is keen of sight, alert, and fleet, and its vocal warnings are effective. But has it other means of detecting, avoiding, or escaping attack by carnivores? Of seeming disadvantage is the lack of a keen sense of smell, and the fact that vicuñas are inactive at night when some carnivores are most active. The habit of walking toward animals that steal nearby in broken cover also seems to be a disadvantage in avoiding predators. In fact, this habit would appear to invite the attack of a puma in ambush. On the other hand, the tendency to rest high on a slope at night might be of defensive advantage. And the reaction of gathering close together in alarm could also be of survival value, for a close group of vicuñas presents an imposing and confusing target to an enemy.

The condor of South America is said to kill mammals such as lambs, calves, young alpacas, and sea lion pups on occasion, but direct evidence of killing is generally lacking. I doubted that condors would kill the healthy newborn of any large mammal until I made the following observation.

One morning in February I watched a vicuña give birth. Within a minute after the infant dropped to the ground two pregnant females of the band (the only pregnant members) dashed to a point near the new mother, the other members of the band (the male and 2 females with juveniles) fled from the site, and 5 adult condors landed 10 yds uphill from the newborn. The mother stood beside her youngster while the two pregnant females pranced between her and the condors, facing them. A few minutes later 9 condors stood on the slope, and some approached the newborn to a point only 2 yds distant. The pregnant vicuñas, tails high, made short charges at the birds as if to strike them with their forefeet, and they drove one vulture into the air. Soon the mother lay down, but she rose quickly when a condor swooped close. At the time that the juvenile first struggled to its feet 12 condors stood on the hillside. Approximately 20 minutes after the birth, 14 condors stood at distances from 20 to 60 yds from the infant. Then several flew. Next an immature condor landed 20

yds from the mother vicuña. The two pregnant females rushed a few yards toward the bird and stood, tails high, and the condor walked away. Soon the remaining condors took off a few at a time, the last 2 departing half an hour after the birth. By that time the juvenile had gained enough strength and coordination to stand with fair steadiness.

In the foregoing observation, it appeared that the danger from condors was greatest when the youngster was most helpless and was slight after the youngster could walk about. In effect, the driving back of the condors by the pregnant females is an example of the direct aid of one member of a species by others. However, the females may have been reacting to the presence of the condors, not to the mother in distress. In another observation, a condor landed near a band and one adult vicuña ran toward the bird and flushed it.

At Huaylarco, commencing at about the time that the first young vicuñas were born, I sometimes saw groups of condors, as many as 14 at once. It is probable that this gathering of condors was in response to an increased number of carcasses in the area. Whether or not condors kill infant vicuñas, at the season of birth the mortality of juveniles and mothers is doubtless high. There may well be a seasonal movement of condors from the seashore in winter to the highlands in summer in correlation with changes in the supply of food, which seems to be principally carcasses of wild animals. Llamas, alpacas, and perhaps other domestic animals bear young at about the same time of year as vicuñas. But in the Andean highlands domestic flocks are closely watched by their herders, and not even a stillborn lamb is likely to be left for condors by the thrifty Indians.

Alarm

Causes and reactions.—Vicuñas are most often alarmed by the approach of men, dogs, or livestock. When a man walks toward a band the usual sequence of events is as follows. The male faces the man and gives the alarm trill. Prone vicuñas rise. Females and young gather into a close group and the band moves away uphill in file, the male in the rear. From time to time a vicuña, usually the male, stops and stares back at the intruder. Generally a band first starts away when a man reaches a point about a quarter mile distant. The group may at first run, then walk, until half a mile from the man before stopping. Male troops usually allow approach to about half the distance that a band permits. Yet, on occasions, even troop males stop grazing to stare at a man walking in the far distance.

A dog causes vicuñas much greater alarm than a man. In one observation, the 3 members of a band were grazing when suddenly one, then all, galloped away at high speed. A dog pursued them closely. The fleeing group drew near a second band, which fled uphill, and the dog raced on past in pursuit of the first group. A few hundred yds farther on one of the fleeing vicuñas turned aside uphill, and the dog continued after the remaining two. These galloped easily, keeping well ahead of their pursuer. They ran across a flat and up a rocky slope, half a mile from their starting point. At the foot of the slope the dog gave up the chase.

Vicuñas may be alarmed by a dog though it is not aggressive, as illustrated by the following account. One morning I released a large black dog from a steel trap set for a fox. Weak from exposure, the dog lay quietly on the ground until late afternoon; then it walked toward its home. The male of a vicuña band, a quarter of a mile distant, trilled and stared at the dog, and as it neared, the band walked away. Then, when the dog reached a point about 200 yds distant, the vicuñas ran up a slope, over a ridge, and out of their territory. But taking no notice of the vicuñas, the dog trudged straight home. On other occasions, however, the sight of an unaggressive dog seemed to alarm vicuñas no more than the sight of a man afoot. One band took alarm and bunched when a dog approached to a point 300 yds distant, but then the group allowed it to trot past 150 yds downslope from them. The dog showed no interest in the vicuñas, and they merely walked a little higher on the slope as the dog passed. The barking of a dog that is out of sight, or at long distance, does not strongly alarm vicuñas, although the sound may draw their attention for a moment.

Normally vicuñas retreat when a llama train approaches to a point a few hundred yds distant. But an exceptionally tolerant male, without a family, remained prone while 20 llamas and 2 Indians walked past on a road only 100 yds away. Although the Indians who herd llamas are somberly dressed, quiet, and almost hidden by the tall llamas ahead of them, vicuñas are more alarmed by llama trains than by grazing llamas alone. Perhaps vicuñas associate the trains with dogs, gunfire, or pursuit.

Mild and strong alarm.—In mild alarm a vicuña stops grazing and stares toward the intruder for a few seconds. Prone individuals may rise but they soon lie down again. Adult males may trill. On occasions, after a mild alarm a band walks away for a distance of about 50 yds, as if to play safe when in doubt concerning the harmlessness of the intruder.

Strong alarm is caused by the attack of a dog. During a period of half an hour a single dog can drive all the vicuñas from an area of a few square miles. On morning while I was watching 3 bands which grazed on a pampa surrounded by low hills, one group started to run. It fled northward, up and over a low hill. Two minutes later the second band took flight. It fled over another hilltop, 300 yds from its starting point. The last group galloped eastward along foothills and up a steep slope. From the south end of the pampa 2 more bands fled northward. Then I saw the cause of alarm—about 600 yds behind the last band of vicuñas ran 2 black dogs. These were more than half a mile distant from the vicuñas when they first took flight. Twelve minutes after the start of the action all of the vicuñas, as well as the dogs, had run out of my sight.

The tendency for the members of a group to stay together in alarm seems to be stronger among vicuñas than among llamas, but weaker than among alpacas or sheep, and this tendency is stronger in bands of vicuñas than in troops. In times of strong alarm animosity between normally hostile groups of vicuñas disappears, and bands may join each other or fleeing troops of males. Here is an example. A troop of 10 males fled over a ridge into an occupied territory and stopped there on a hillside. Then over the ridge came running two dogs, closely followed by a third and a horseman. The resident band fled uphill and joined the troop of males, and together the 2 groups raced across the slope. Two more vicuñas joined them. Finally the mixed group stood on a rockslide high on a slope, while the horseman and his dogs moved on past.

Return after strong alarm.—At an interval of from one to several hours after a band of vicuñas is driven from its territory the group returns. For example, at about 8:30 one morning a man walked through the territories of bands A and B and the vicuñas fled. Two hours later neither band had returned, but by 3:00 p.m. both groups had returned and were grazing at customary sites on their territories. On another occasion, dogs chased bands A and B from their territories at 7:30 a.m. The first band returned at 1:35 p.m., the second an hour and a half later. In general, bands disturbed in mid-morning return to their territories by mid-afternoon, and those displaced in mid-afternoon return by sunset.

The return of displaced bands to their territories is leisurely. In one observation, a band ran a few hundred yds out of its territory and to the crest of a ridge as an Indian with his llamas walked by. The herdsman did not pause, but the vicuñas made no attempt to descend the slope during the next hour. In another observation, a band returning to its territory loitered for two hours on the territory of an adjacent band, which was absent. Return to the territory after alarm seems to be more rapid in the late afternoon than in the morning, as if evening hunger stimulates movement back to the home pastures. If a troop of males is driven up a rocky slope by dogs or men in the morning it may not come down to lower pastures and better forage until 2 hours later, but if driven onto barren ground in the late afternoon the males may return downslope within half an hour.

Bands or members that are disturbed late in the afternoon or at night normally return to their territories the next morning, within 2-3 hrs after sunrise. Sometimes the delay is longer. One evening I watched bands A and B bed down for the night. At daybreak the following morning band B was not on its territory, and two members of band A were absent. One of the missing members of A returned at 9:00 a.m., the other at about 4:30 p.m. The male of band B returned at noon, and his females soon followed.

Even when disturbance is strong, prolonged, or repeated on successive days, vicuñas return to their territories soon after the annoyance ceases. For a period of a few weeks in spring, livestock grazed nearly every day on the territories of bands under study at Aricoma. The stock reached the study area some time after 8 o'clock in the morning and departed before 5 o'clock in the afternoon. During the daylight hours before and after stock occupied these territories the resident bands of vicuñas grazed there.

At Huaylarco, during a period of 2 months, a dozen road workers camped just outside of my study area and frequently disturbed the vicuñas. Nearly every day these men walked close past vicuña territories along the road, and they spent many hours at a time working with picks and shovels nearby. When the men walked past the bands of vicuñas usually fled, and they could not be seen from the road for hours afterward. But in the late afternoon, about 2 hours after the workmen had departed for the day, nearly all of the resident vicuñas could be counted on their territories from points on the road.

The displacement of bands from their territories has important effects on the supply of forage. For the few hours that the resident band is absent the territory is relieved of grazing by that group, which feeds elsewhere. But while the band is absent large numbers of livestock or troops of male vicuñas may graze on the territory and deplete the forage rapidly.

Cautiousness.—Troops of males generally allow closer approach than family bands. In part, this tameness is due to the youth of most troop members. Yearlings and juveniles are less wary than older vicuñas and may not react to a disturbance that causes adults to stare. In bands the most alert member is the male. If he permits, the band usually can be approached to a short distance. The alertness of the male does not seem to depend on the size of his family, for a solitary resident male may be more wary and vociferous than a male with several females. Even after we had camped for 3 months near the territory of one lone male, he trilled at me when I was 600 yds off, and he fled when I approached to 400 yds.

In one observation, a female proved more wary than the male. She was a new member of the band and apparently unaccustomed to men. Early one morning I walked, in my customary manner, to a rock shelter at moderate distance from the band. On many previous days the band had paid no attention to my approach, but this time the new female stood up and gave a squeal of alarm. Not until then did the male trill and the other females stare.

Vicuñas that dwell far from roads or trails seldom encounter people; consequently, they are shy. One vicuña band at Aricoma lived in an amphitheatre 2 mi from the nearest road or llama trail. On occasions when I approached to a distance of half a mile downslope from the band, it retreated uphill. One morning I stalked to a point 500 yds distant from this band before I lifted my head above the intervening rocks. The vicuñas stared toward me and started uphill. I hid immediately, but 20 minutes later the band was a quarter of a mile beyond its starting point and still walking away. Near certain sulphur mines,

and in other areas where men hunt from automobiles, vicuñas are much more wary than those studied at Huaylarco. These vicuñas will flee if a car stops several hundred yds away.

Although it is said to be difficult to force llamas or alpacas to rise when they are resting at night, wild vicuñas are cautious at night and easily take alarm. On one occasion, by moonlight, one and one-half hours after sunset, I stalked a resting band of vicuñas. I was able to reach a point no closer than 200 yds from them before one rose and gave the alarm trill. It soon lay down again. On another occasion, two hours after sunset, the reaction was similar except that the group ran away from me. Apparently vision is adequate for running in darkness. Sometimes while driving at night I saw by the headlights the pale red eyeshine of a group of resting vicuñas. The animals stood for a few seconds as if confused, then ran off into the night.

Tameness.—Bands of vicuñas become moderately tame through long peaceful association with man. At Aricoma bands A and B lived close to our camp for a period of 5 months. Several weeks after we arrived they grazed as close as 50 yds from the stone walls surrounding our campsite. On a few occasions, one of these bands rested all night on slopes 100 yds from camp. Near the end of our stay these vicuñas showed no alarm when I walked toward them in the open to a point 200 yds distant. Sometimes they stared, but did not run, when I approached to a point 50 yds closer. Late in the afternoon, when vicuñas are bold, I once sat quietly on open ground while band A walked past me at a distance of only 80 yds. In many areas where vicuñas see harmless men nearly every day, they seldom retreat from a man afoot until he reaches a point less than one-quarter mile distant.

A man that walks toward a group of vicuñas from a usual direction causes them little alarm, as compared to a man that approaches from another direction. For example, after several weeks of observing bands A and B from a small rock house, I could incautiously walk to that house, sometimes only 50 yds from the vicuñas, without alarming them, provided that I traveled a certain path. But if I approached from another sector members of these bands became alarmed when I reached a point about 200 yds distant. Probably because they approach from a familiar direction, men walking on a road cause only moderate alarm in bands of vicuñas. In areas of much foot traffic, a man can walk along a road to a point about 200 yds from a band of vicuñas before they show alarm, and they may not retreat until the man is 100 yds away.

Cars on the road alarm vicuñas much less than cars traveling cross-country. In one observation, I parked my jeep 300 yds from a large band of vicuñas, which stood at the edge of a road. They took little notice of me, but soon walked a short distance away from the road. I then drove over the grassland to a point 300 yds from them. The vicuñas ran in alarm but finally stopped. Again I drove toward them. This time they retreated to a distance of 500 yds. Yet, even far from roads vicuñas are less alarmed by a car than by a man on foot. Driving over pampas in a jeep, I was often able to reach a point less than 200 yds from a group of vicuñas before they started off. And on occasions when I parked for a long period, using my jeep as a blind, troop males wandered as close as 20 yds and band females grazed within 50 yds.

Probably roadside bands are less alarmed by a car than by a man afoot because they are familiar with cars as normally harmless objects that pass on an established path. At Huaylarco, resident bands sometimes did not retreat when a truck passed only 50 yds away, but a man could walk to a point no closer than two or three times this distance before the vicuñas retreated. Continously moving cars cause less alarm than cars that stop. When a car stopped nearby most vicuñas close to the road at Huaylarco retreated to points at least 100 yds distant. For this reason, tourists who stop their cars to photograph vicuñas usually secure only disappointing rear views.

Vicuñas seem to be as tame toward a group of men as toward a single man. In one observation, a truck loaded with Indians drew near to a roadside band of vicuñas. A few of the animals retreated several steps when the truck was 400 yds away. To allow the vehicle to ascend a grade, 30 men clambered down from the truck bed and walked up the hill. The vicuñas showed little additional alarm. They walked away from the road and grazed only 200 yds from the crowd. On many occasions, I noted that bands of vicuñas continued to graze in spite of the fact that several men were digging on a road 200 yds distant.

Surprise.—Vicuñas are nervous creatures. Even when there is no apparent cause for alarm, all the members of a band may suddenly run a few steps. Then half a minute later all graze calmly. Not only do they burst into a gallop at the sudden appearance of a man or dog at short distance, but they are startled by any sudden movement or sound. A juvenile may start when a finch takes flight nearby, or when a butterfly or wind-borne leaf passes. The sudden whir of a flock of seed snipe taking wing causes vicuñas to raise their heads quickly and stare toward the birds. Often I saw a group of vicuñas run a few steps when a flock of geese glided close over their heads. An adult vicuña drew back hurriedly from a goose that apparently hissed, and a juvenile which was chasing a goose retreated when the bird flapped its wings. One adult male ran a few yards when a loudly calling lapwing swooped close over him. Any close object that moves suddenly causes vicuñas to gather together, to stare at the object, and perhaps to run a few steps.

A similar reaction occurs when vicuñas are surprised by a loud sound, whether it be a sneeze, a clap of the hands, the starting of a car engine, or a distant gunshot. At the sound of a shot from a small caliber rifle 200 yds away one band ran a distance of 150 yds and up a slope. As toward other disturb-

ances, troops react less than bands to a sudden noise. In one observation, I saw a man in a truck shoot again and again at a troop of males 200 yds off. The males walked slowly away showing little alarm.

CURIOSITY

Inquisitiveness toward men and dogs.—Vicuñas are strongly inquisitive. They may walk toward any moving object that is partly hidden, as if to identify it by closer inspection. Thus, the first reaction of vicuñas to a man stalking them is to move toward him. Once as I was sneaking toward a large troop of males, they detected me at a range of 100 yds and then walked 50 yds toward me, craning their necks, peering. Suddenly they dashed away, halted, turned about, and walked to a point even closer to me than before. As I crawled away some of the males raised their heads above the level of the intervening ground and stared at me. In another observation, a family band that detected me at 300 yds distance ran 30 yds toward me, the male coming nearest. He stood and stared in my direction for a time and then lay prone facing me, alert. It was not until a quarter of an hour later that he rose and grazed. On one occasion, band A walked toward me until it reached a point only 50 ft from the rock wall behind which I was partly hidden, and one member of the band trilled repeatedly. Another time, as I was stalking an irritable lone resident male on open ground he discovered me. I sat quietly on the grass and he walked toward me, trilling again and again, until but 70 yards distant. Even when the band male is absent the band females may walk toward unrecognized moving objects, but their approach is not so ready or so close as that of the male, and their curiosity is more quickly satisfied.

If vicuñas see a dog standing or walking in the open at long range they stare at it, walk toward it, and trill, as if they are curious rather than alarmed. In one observation, a band was grazing when the male spied a dog lying down 300 yds away. He gave the alarm trill, walked a few yards toward the dog, stood for a moment, and then repeated these actions again and again until he was 100 yds closer. Before he resumed grazing this male stood at one spot for a period of 10 minutes trilling at intervals of 10-60 seconds. In another observation, a family male walked toward a dog and took a stand between it and his females. The dog walked on past, 100 yds from the vicuñas, and the male vicuña walked parallel to the path of the dog for a distance. Such reaction to a passing dog is similar to the usual reaction to a nearby fox.

Following foxes.—The vicuña behaviorism of investigating obscured moving objects might have evolved as a response to the approach of foxes or other predators. If a fox walks within sight of a band of vicuñas the male gives the alarm call and walks toward it, and his females may follow. Here is one example. A band had been grazing for some time when abruptly the male started walking straight up a slope. The rest of the band followed him. Soon the vicuñas halted and stared toward the foot of a cliff farther uphill. Then, male leading, the band ran toward the cliff. At the base of the cliff the group halted and intently gazed at a fox, which was walking across a slope 30 yds from them. With the male in the lead, tail arched, the vicuñas followed the fox. All of the females but one lagged behind the male; this one accompanied him across the hillside, following the fox. When the fox started to run away the two vicuñas stopped. They had walked about 300 yds from their starting point.

On another occasion, I was watching two bands as they rested at sunrise. All at once a member of one band gave the alarm trill and the group ran 50 yds upslope, the male dashing ahead and stopping on the crest. Then I saw that a fox was walking close to him and heading toward the other band. This group ran toward the fox, halted, walked parallel to the path of the fox for about 100 yds, and stopped again. Several minutes later the same band ran on 75 yds and once more stood and stared at the fox, then about 150 yds distant. The band male continued to stare at the fox as it walked away.

Normally vicuñas do not approach a fox to a point less than 30 yds distant, but in one observation a male and 2 of his females followed a fox at a distance of only 5 yds. When a fox is close at hand some members of the band hold their tails high, or they trill, and they may stand with forefeet atop a boulder as if to get a higher point of view. Usually vicuñas return to grazing by the time that the intruding fox has moved away to a distance of about 100 yds.

Interest in other animals.—The curiosity of vicuñas is further illustrated by their apparent interest in other animals near them. A yearling stared at a mountain viscacha *(Lagidium,* family Chinchillidae) which ran close by and then, ears erect and tail out, walked slowly after it. A short time later this yearling walked 50 yds up a slope in following one viscacha and another, staring at them intently from distances as close as 5 yds. A group of 4 vicuñas, apparently troop males, scrutinized a pair of Andean deer or huemuls *(Hippocamelus)* which walked close by. In one observation, a small band of vicuñas walked up to an aplomado falcon which perched on a low rock near them. One yearling, gazing intently, advanced to a point 3 yds from the bird before it flushed. Then the vicuñas followed its flight with their eyes. In yet another example, 2 female vicuñas stared at a mountain caracara *(Phalcoboenus)* that stood on a low boulder. They walked toward the bird until 10 ft distant; then it hopped away.

Juveniles are especially inquisitive toward smaller animals and sometimes they chase geese *(Chloëphaga).* In one observation, 4 young vicuñas walked 20 yds toward 2 geese and then chased them as they waddled away. Usually, if a vicuña approaches a goose to a point about 5 yds away the bird scampers, flapping is wings but not taking flight. I also saw juvenile vicuñas chase seed snipe *(Thinocorus).* In one instance, a youngster 11 days old rushed at a group of 5 seed snipe on the ground and flushed them.

RELATIONS WITH LIVESTOCK

To the tourist traveling through the highlands of Peru it might appear that vicuñas are compatible with llamas, alpacas, sheep, and other livestock. Even in the mating season, when interspecies antagonism is probably greatest, I saw vicuñas grazing as close as 40 yds from groups of alpacas and llamas. On one pampa where hundreds of alpacas and llamas grazed I counted 75 vicuñas. In general, however, as Sr. Paredes pointed out to me, in mixed groups of lamoids each kind tends to stay with others of the same species.

Disturbance by livestock.—When I commenced field studies of the vicuña at Aricoma in autumn, I did not foresee that livestock, then essentially absent, would be brought from lower levels to higher greener pastures in winter. In mid-August about 100 sheep, alpacas, and llamas, entered my study area, and the Indian herdsman appropriated my rock blind as a home for his family. In early September more stock arrived. Because of these disturbances, we moved camp.

Reconnaissance at Huaylarco in April and again in early October had revealed no livestock save transient llamas. During summer studies there interruptions by livestock were rare until mid-February, when new green forage appeared. Then about 1,000 sheep arrived at pastures near the study area, and a month later more sheep, a few horses, several dogs, and a family of Indians became established within the study area. Fortunately much of the sheep grazing occurred outside of the vicuña territories under study, and the grazing site was changed from day to day. Fortunately too, the vicuñas were not disturbed by livestock early and late in the day, for the sheep were herded into corrals in the evening and not taken out to graze until long after sunrise. As a general practice in the highlands, llamas, horses, and cattle are left on the range at night, so these may disturb vicuñas after dark as well as by day.

Vicuñas do not defend their territories against invasion by livestock. When alpacas or llamas draw near a vicuña gives the alarm trill and stands erect with tail up, but this reaction seems to have no relation to the crossing of the territorial boundary by the invaders. Sometimes a band of vicuñas does not retreat until the intruders are less than 50 yds away, but when the disturbance is prolonged vicuñas may leave their territories even though the intruding livestock is much farther away. In many cases this movement away is probably due not to strong alarm, but to the fact that vicuñas seek more favorable pastures when the usual feeding grounds are disturbed. This idea is supported by the observation that under these circumstances the male normally leads the movement away, whereas when a band retreats in alarm the male guards the rear.

Here are some examples of the reactions of vicuña bands to livestock. One morning a resident band was grazing near the edge of a large flat when 30 llamas and alpacas arrived at a point a quarter mile distant. At first the vicuñas seemed not to notice the invaders, but soon a flock of sheep spread over the flat. The male of the vicuña band stared at a group of llamas 200 yds off, then retired upslope, followed by his family. The band continued on over a ridge and out of their territory. Seven hours later, after the livestock had departed, the same band of vicuñas appeared atop the same ridge, and slowly they decended to graze on the flat. In another observation, 2 alpacas spent the night resting about 400 yds from a band of vicuñas, but on another territory. In the early morning, shortly after the last member of his band rose, the male vicuña gave a screeching call toward the alpacas. Then the band walked away from them a distance of 100 yds and grazed. Normally at that hour the band moved toward the site occupied by the intruders.

That a single alpaca may chase resident bands of vicuñas from their territories is illustrated by an observation made at Huaylarco one morning in April. At 6:15 a.m. a resident band was grazing on a grassy pampa bordered by low barren hills. From the hills came a large, black and white, male alpaca. When he reached a point 200 yds from the vicuñas they stared at him and walked away. The alpaca defecated on a dung pile, nosed it, and then ran toward the vicuñas. When he reached a point about 100 yds from them they retreated a short distance. A few minutes later, after stopping at two more dung piles, the alpaca ran 50 yds toward another resident band of 25 members. At first these vicuñas retreated at a walk, but when the alpaca reached a point 300 yds from them they ran a few hundred yards away, finally stopping on low bare hills at the edge of their territory. After voiding again, the alpaca once more galloped toward the 25. They retreated another few hundred yds across the barren slopes until they were well outside of their territory, a third of a mile from their starting point. This entire action took place in 17 minutes. Half an hour later the alpaca returned to the grassy pampa, where the first band still grazed. When he reached a point about 100 yds from them the vicuñas ran from the pampa to barren ground. At last the alpaca grazed alone on the flat, which was normally occupied by the two resident bands of vicuñas.

Competition for food.—Several kinds of wild and domestic animals graze the same pastures as vicuñas. The principal wild animals that compete with vicuñas for food are the huemul, guanaco, viscacha, and Andean goose. Although the over-all competition of these with the vicuña is minor, they may consume much forage on certain sites. The huemul is found in grassland hills near cliffs. Guanacos occur throughout the vicuña zone, including the driest parts, but they are not common. Viscachas feed on nearly all plants that grow near the rockslides in which they dwell. And flocks of as many as 100 Andean geese graze on damp pastures in vicuña territories.

The domestic mammals that compete with vicuñas are: llamas, alpacas, sheep, cattle, horses, and mules. Only the first three are of major importance on vicuña range. In the Inca era llamas were probably much

more numerous than now, and alpacas were common. Since then horses and mules have largely replaced domestic lamoids as cargo beasts, and sheep and cattle as producers of wool and meat. Yet, llamas are still common in all parts of the vicuña range. Almost every day of our stay at Huaylarco and at Aricoma trains of as many as 50 llamas passed by. In southern Peru the network of llama trails far exceeds the system of automobile roads. Furthermore, many herds of llamas graze in the highlands in semi-freedom. Possibly there are as many llamas as vicuñas in the range of the latter. In the region of the center of the vicuña range, in Peru and Bolivia, alpacas are raised on a large scale and they far outnumber llamas. Flocks of alpacas generally dominate the wetter pastures where grasses are lush.

Sheep were introduced in the Peruvian highlands by the Spanish in the sixteenth century. This event has probably resulted in a reduction of the forage available to vicuñas, for the preferred foods of sheep and vicuñas appear to be much the same. Sr. Paredes, who keeps thousands of Corriedale sheep as well as vicuñas, recognizes no difference in the food habits of the two animals. That vicuñas compete with sheep for grass is corroborated by Dr. D. F. Watson, veterinarian, of La Oroya, Peru. He informed me (letter, 1955) that in central Peru large groups of vicuñas graze in the sheep pastures of the Cerro de Pasco Corporation, and that in this region it is claimed that vicuñas consume pasturage which would support several thousand sheep.

In the course of four centuries, it is probable that sheep grazing has caused notable changes in the grasslands of the puna. The present striking dominance of coarse bunch grasses might be, in part, the result of heavy utilization of more succulent plants by sheep. In addition, constant disturbance incident to sheep herding might have forced vicuñas out of much of the lower part of their former range. The present competition between sheep and vicuñas is reduced by two factors: first, sheep are seldom pastured in the drier, higher, and more barren parts of the vicuña range; second, sheep generally graze the same pastures as vicuñas during only a few months of the year. At Aricoma sheep grazing was significant only in winter, and at Huaylarco only in summer, while at Cerro de Pasco vicuñas are found principally on pastures that are being rested from sheep grazing. Were it not for these factors that reduce the intensity of sheep grazing in the puna, the forage available to vicuñas would probably have long since been depleted. It is apparent that research on range conditions and trends, especially in their relation to wildlife, is greatly needed in the grasslands of the Andes.

HUNTING, UTILIZATION, AND MANAGEMENT

Hunting Methods

History.—Because of their fine wool and delicious meat, vicuñas have been hunted for centuries. In his chronicle of travels through the Inca empire in the middle of the sixteenth century, Cieza de León (Markham's ed. 1864:288) describes the royal hunts of which he was told. On order from the Inca, as many as 20,000 Indians on foot surrounded a large area and converged toward the center, driving the game before them. With clubs, the men killed as many as 10,000-15,000 trapped animals. Presumably these included vicuñas, for in the same paragraph the author mentions vicuña wool.

Somewhat later, in the last half of the sixteenth century, Garcilaso de la Vega (Markham's ed. 1871:115-117) lived in the region of Cuzco, Peru. He also describes Inca hunts of "former days," apparently deriving his information from interviews with older residents. This author relates that for a "chaco" the Inca hunting party ordered out 20,000-30,000 Indians. These formed a circle 20-30 leagues (about 60-90 miles) in circumference and then closed in, taking game by hand. Sometimes 20,000-40,000 animals were captured. Many of these were killed, but guanacos and vicuñas were shorn and freed. In order to allow the fleece to grow, hunts in each district were made at intervals of 3 years and alternate areas were hunted in intervening years. Except in these hunts, the Indians were not permitted to take game. In all, the Inca system seemed to be sound game management practice.

The Spaniards hunted with dogs at an early date, for Garcilaso *(op. cit.*:383) states that guanacos were hunted with greyhounds in his time. Guns, too, were used in hunting, for the same author wrote, in 1602, that scarcely any guanacos or vicuñas were left except where it was difficult to use guns. It seems, however, that vicuñas were not well known at first hand by Garcilaso de la Vega, because for basic information he draws on the writings of Acosta.

Father Joseph de Acosta (Markham's ed. 1880:287) lived near Lake Titicaca in the 1570's. He complained that because the Spaniards allowed too much hunting of vicuñas the numbers of these animals had been much diminished. Judged by the accounts of this author, chacos were much smaller than under Inca rule. Still, 2,000 or more Indians participated in a hunt. These men captured 300-400 vicuñas, killed what they wished, sheared some, and released many, especially the females. Some vicuñas were taken with the bolas. In Acosta's time vicuñas were esteemed for the bezoar stones that were occasionally found in their stomachs. These stones were believed to be highly effective medicine against poisons and disease *(ibid.*:293).

Nearly three centuries after Acosta's time, J. J. von Tschudi (1847:313-314) found the chaco method of hunting still being used, but with the addition of a corral. He tells of a hunt in which about 80 men built a corral half a league (about 1.5 miles) in circumference of tall stakes. Ropes hung with colored rags connected the stakes. The men drove vicuñas into the enclosure, captured them with bolas, and killed them. Then the stakes and ropes were taken to another site and the hunt was repeated. In a chaco in which Tschudi took part, 122 vicuñas were taken

during a period of 5 days. In Tschudi's opinion, frequent hunting was not diminishing the numbers of vicuñas. He stated *(ibid.*:315) that in "former times" they were hunted more than about 1840. Yet, according to Cabrera & Yepes (1940:269), one author of the early nineteenth century calculated that about 80,000 vicuñas were killed annually in Peru and northern Chile.

The great slaughter of vicuñas continued into the early part of the present century. Madueño (1912:-28) reports that the official figures for the export of vicuña wool from Peru from 1902 to 1907 are 19,409 kilos (about 43,000 lbs) of wool and 14,534 kilos of dried skins. This export represents the wool of about 50,000 vicunas, all presumably killed—and the number does not include unreported exports or consumption within the country! Evidently the high rate of killing went on for another 20 years, for in 1926 Peru exported 2950 kilos of vicuña wool, the fleece of about 5900 animals (Cabrera & Yepes 1940:269).

In Argentina, too, vicuña hunting was intense and great numbers were killed (Romero 1927:154-155). The young were hunted with dogs, and older vicuñas with guns. Romero states that with dogs and bolas, one man could catch a vicuña by stratagem. In some areas a corral method of hunting was used. Presumably these methods persisted in Argentina until general hunting of vicuñas was prohibited, in 1926. Within a few months after the new law went into effect, the bedspread makers of La Quiaca obtained 1200 skins of vicuñas that had been taken before the prohibition *(ibid.*:149).

Present hunting.—The capture of infant vicuñas is said to be common practice among the highland natives of Peru. Within half an hour after birth a newborn vicuña can easily be taken by hand. Once an attempt to capture an agile youngster was witnessed. A truck, loaded with Indians, stopped near a band of vicuñas. Several men jumped from the truck and ran to a point between the main cluster of vicuñas and two that stood 100 yds from the others. These two were a tiny juvenile and its mother. The men knew vicuñas well, for the mother and young ran straight toward the rest of the band. In so doing they passed through the group of men who grabbed at the infant. A less agile youngster would not have escaped their hands.

On several occasions I saw a man shooting at vicuñas from a car or truck on the road. The usual weapon was a .22-caliber rifle. A small pistol was used by one American tourist who boasted that he shot at vicuñas near the road thinking that they were deer. Inasmuch as a vicuña hit by a small bullet rarely drops immediately, and as roadside hunters are impatient and lazy, these men commonly wound several vicuñas before one falls near the road. A hunter on foot has difficulty in closely approaching family bands, which are warier than male troops. But in a car one can easily approach bands of vicuñas to a point within range of a small rifle. In all, hunting from cars is more harmful to vicuñas than hunting afoot, for the road hunter shoots wantonly, wounds many animals, and hits a relatively high proportion of females.

Violation of laws prohibiting the shooting of vicuñas is widespread and frequently open. Near one camp in Peru, two uniformed members of the Guardia Civil of a nearby town killed one vicuña and shot at others. For weekend diversion these men, using large-caliber government rifles, shot at nearly every large animal that came within range. Nevertheless, they complained that the Indians killed many young vicuñas for their hides. At a mining camp where I was a guest, vicuña meat was a common item on the bill-of-fare. Once at Aricoma and twice at Huaylarco I came upon an Indian with a gun stalking vicuñas. Members of a road crew begged me to shoot vicuñas for them or to lend them my rifle for this purpose. Several persons told me that much of the dried meat sold in the public markets in southern Peru is vicuña charqui. Even in the highlands near Lima, where law enforcement should be most effective, one resident informed me that a fair amount of illegal hunting takes place. In Antofagasta, Chile, sulphur miners admitted to me that they often shot vicuñas for meat. An Argentine zoologist wrote me that in his country too, there is no strict compliance with protective laws.

In remote areas where fresh meat is scarce, one can hardly blame local natives for killing vicuñas to obtain meat and hides for their own use. The Indians prefer vicuña meat to any other kind. The flesh, similar to that of alpaca, is considered "muy rico" as compared with huemul (deer) venison, which is "muy seco." As sleeping mats some men use the hide of a vicuña instead of the usual sheepskin. (In many regions the Indians are so needy that it was impossible for us to keep our garbage buried. They dug it up to salvage empty condensed milk cans.)

In total, it is improbable that pastoral Indians greatly reduce the vicuña population by shooting. Because of the expense and legal complications of obtaining guns, few Indians have them. The guns they do have are normally low-powered single shot arms, often muzzle loaders. Further, an Indian usually kills but one animal and this he utilizes fully before he hunts another. Lastly, as Indian hunters are more likely to get within range of an immature male than within range of a female, they kill relatively few females.

One day I observed an ingenious hunt by two Indians. While I was watching several bands of vicuñas which grazed on a wide pampa, a man walked quietly past them at a distance of a quarter mile. Upon reaching the edge of the pampa the man ascended an isolated ridge-topped hill a few hundred feet in height. Some time later, a boy came from the same direction that the man had come. But instead of following the route of the man, he walked directly toward the bands of vicuñas and the hill beyond them. The band nearest the boy ran toward the hill. Other

bands, closer to the hill, stared at the approaching runners, then turned and fled for the hill. When the bands were part way up the slope they paused for a while, then continued upslope as the boy ran toward them. The vicuñas reached the crest of the hill, half a mile from the starting point of the first band, less than five minutes after the initial alarm. Soon they ran along the narrow crest of the ridge and past a group of rocks, behind which the man had taken a stand with his gun. When the vicuñas had passed, the man ran after them, gun in hand. Evidently he shot at least one, for a few hours later I found a dead vicuña, freshly shot, near the site.

LEGAL PROTECTION

Protective legislation.—During almost 300 yrs of Spanish domination in Peru the persecution of vicuñas was apparently extensive and unrestricted. But some people realized the danger of exterminating the vicuña for, in 1825, soon after Simón Bolívar liberated Peru he issued decrees prohibiting the killing of vicuñas and offering a reward for each one domesticated. The text of these decrees is given by Cardozo (1954) and Maccagno (1932). That this law had little effect is evident from Tschudi's account of taking more than 100 vicuñas in one hunt in the 1840's. The decrees of Bolívar were reaffirmed by the government about 1900, but a more inclusive law was not passed in Peru until 1920. This Peruvian law prohibited not only hunting but all commerce, manufacture, and use of vicuña hides, wool, and fabrics. That the regulation was eventually effective in restricting legal export is shown by the fact that only 60 kilos (about 130 lbs) of wool was exported in 1928 (Cabrera & Yepes 1940:269). Later laws (1936, 1940) reaffirmed and modified the prohibitions. Under special permit and supervision one can raise vicuñas and shear them, but anyone buying or selling vicuña wool must first obtain written authorization from the government. Further, the exportation from Peru of living vicuñas or other lamoids is prohibited, except by special permission.

In Argentina the hunting, export, transit, and sale of vicuña hides or wool was first prohibited in 1926. Cardozo (1954) and Romero (1927) give the text of the decree. This law also provided for legal hunting of vicuñas in certain zones and seasons.

In Bolivia, too, the hunting of vicuñas is illegal, but the manufacture and sale of articles made from "imported" vicuña hides or fleece is a thriving industry. This legal situation would seem to be an invitation to unlawful killing of vicuñas in Bolivia, smuggling of hides from Peru and Argentina, and bribery of border officials. In La Paz, Bolivia, tourists may buy robes made of vicuña hides. Some of these "colchas" are made entirely of the fleece of the necks or legs of infant vicuñas. Cardozo (154:118) tells of one made from the necks of 77 young. These robes, accompanied by a certificate of Bolivian origin, are allowed to pass through Peru. According to Dr. George Bevier of the Rockefeller Foundation in La Paz (letter, 1953), the only real control on this traffic in vicuña products is a tax, and the limitation of export to one robe per passport. It is also unlawful to hunt vicuñas in Chile, but the animals live so far from centers of population that this law cannot be enforced.

Illegal trade.—Although trade in vicuña articles is unlawful in Peru, I had been in the Lake Titicaca region only a few days before a uniformed road control official tried to sell me the hide of a vicuña. Later I had opportunity to buy many vicuña hides. In June, 1951, a new robe made of the skins of 16 infant vicuñas was offered for sale to Dr. Duffie, of Juliaca, for approximately $20.00. The Duffies told me that nearly every week at that season they saw other vicuña products for sale.

The only man in the Lake Titicaca region who can legally sell large quantities of vicuña wool (ranch-raised), and is therefore in position to hear of illegal trade, is Sr. Paredes. He told me that thousands of young were killed each year, and that their hides were smuggled into Bolivia. In April, 1951, the majordomo of a group of roadworkers at Huaylarco told me that almost every day young vicuñas were caught there by transient Indians, and that the hides were sold in border towns. As there are more vicuñas in Peru than in Bolivia, in all probability many "Bolivian vicuña" articles are made from hides smuggled out of Peru.

WOOL

Under Inca rule, sacred matrons dedicated to the service of the temples of the sun wove fine vicuña cloth for royalty and for the ornamentation of temples (Cieza de León 1864:405). Today vicuña wool is prized throughout the world for luxury fabrics. According to Stroock (1937), a New York manufacturer of vicuña fabric, the wool "combines to an extraordinary degree practically every essential of texture, lustre, tensile strength, and beauty."

Vicuña wool is by far the finest and softest fiber used in wool manufacturing. According to figures in the American Wool Handbook for 1948, for 1100 fibers measured, the average diameter was but 13.2 microns (dispersion 6-25 microns). Fine merino sheep staple averages about 22.8 microns in diameter. In a wool quality grading system which is based on the finest possible count to which the fiber can be spun, fine sheep wool is of grade 62s to 64s, and llama and alpaca wool between 56s and 60s, but vicuña wool grades from 120s to 130s.

The principal defect of vicuña wool is that the fine hairs are mixed with coarse hair, except on the back of the animal (Romero 1927). For this reason, it is the practice on Sr. Paredes' ranch to shear only the back. But this practice results in low wool production, one-quarter to one-half pound of wool per animal per year. At this rate, a vicuña produces only 2-4 lbs of wool in its useful lifetime, about 8 years. If, however, a vicuña is not sheared every year, and if some coarse wool is taken, the fleece may weigh a pound. Another defect of the wool is that the

staple is short, about two inches in length, so that it is difficult to weave by some processes. And furthermore the wool is highly resistant to the penetration of dyes.

Because of low wool production, manufacturing difficulties, and export taxes, vicuña fabrics are costly. In Peru in 1949, Sr. Paredes sold the raw wool for $10 a pound. The retail price of vicuña cloth in Lima, in 1952, was $66 a yard. The price is much higher in the United States—$110 to $250 a yard for heavy-weight overcoating (Stroock 1937). An overcoat requires the wool of about 40 vicuñas and costs, in New York, approximately $800 (1953).

Vicuña wool is also prized by the highland people of the Andes for making ponchos, scarfs, and sweaters. The manufacture of vicuña skin articles especially bedspreads, was an important industry of the Indians of Peru and Argentina before the prohibition of vicuña hunting. This industry still thrives in Bolivia.

DOMESTICATION

Pets and zoo specimens.—Young vicuñas make tractable pets. In the Lake Titicaca region I often saw one or two young vicuñas in a market place, village square, or hacienda yard. Vicuñas do fairly well in zoos. The New Zoological Park has had 13, 5 of which were born there, and it still has 3 (R. M. McClung, letter, 1953). Several other zoos have living vicuñas.

Domestic flocks.—Pointing out the docility of pets as examples of the ease with which vicuñas are domesticated, Simón Bolívar and various South American agricultural authorities (Romero, Maccagno) have urged the domestication of flocks of vicuñas. During the Spanish viceroyalty, the Jesuits in Peru are said to have built up a flock of 600 vicuñas, but these were abandoned when that religious order was expelled (Madueño 1912:12).

The foremost vicuña rancher in southern Peru, Sr. Paredes, has raised vicuñas since 1919. In 1951 his herd contained about 400 animals. Shortly after the young are born, the vicuñas are driven into corrals where they are lassoed and sheared. These operations have yielded several hundred pounds of wool. In spite of his success in rearing vicuñas, Paredes' venture is a hobby which has not repaid its cost. Sheep raising brings him far greater profit.

One difficulty with vicuña raising is that the animals cannot be handled like cattle or sheep. Even pets usually become vicious when they reach maturity. At Calacala most of the males must be castrated to prevent fighting. Whenever I closely approached a tame vicuña at Calacala, it spat or kicked at me. Groups in fenced pastures are intractable. At Calacala I watched a line of 15 men, about 30 yds apart, try to drive 150 vicuñas the length of a walled pasture and into a corral at the end. They corraled only a quarter of the animals. Paredes told me that on one occasion he left a group of vicuñas in a corral overnight during a storm. In the morning more than 20 were dead. Evidently the storm frightened them and they dashed against the stone walls of the corral.

Although I saw not a single fight between a male and female vicuña in the wild, when the sexes are confined together they often fight. A pair at the National Zoological Park could not be kept in one cage because the male attacked the female (W. M. Mann, letter). I saw males pursue and bite females in a corral at Calacala. In fenced pastures there the sexes are usually kept separate to prevent fighting. When pastured with females, large males are hobbled. At Calacala vicuñas have been raised in domestication for generations, yet they are too nervous and quarrelsome for efficient handling. If vicuñas were amenable to domestication, it is probable that the ancients who domesticated the llama and alpaca would also have domesticated the vicuña.

Hybrids.—The value of combining the high wool quality of the vicuña with the high wool-producing capacity of the alpaca has long been realized. Madueño (1912) describes the historical attempts to establish the paco-vicuña, a hybrid of the alpaca and vicuña, as a breed. The first notable success was that of a Peruvian priest, Cabrera, who in 1845, after 21 years of effort, had built up a herd of 20 paco-vicuñas. For this feat he was given a pension and high honors. Another Peruvian, Belón, had created a somewhat smaller band by 1893. He is said to have succeeded in interbreeding the hybrid paco-vicuñas. Apparently because of the frequent sterility of hybrids and lack of genetic knowledge, no breed of vicuña hybrids has yet been produced, but efforts continue. In 1951, at a branch of the Granja Modelo of Puno I saw about 100 white alpacas with half as many vicuñas in a large fenced pasture. The vicuñas, many already hybrids, had been acquired by purchase a year earlier. At the time of my visit no offspring had yet resulted from this hopeful mixture.

At Hacienda Calacala the first paco-vicuña was born in 1931. Twenty years later Sr. Paredes had approximately 50 hybrids resulting from crosses of vicuñas with alpacas, llamas, and paco-vicuñas. To produce a paco-vicuña, Paredes' system has been to raise a young female alpaca with a young male vicuña, initially feeding both on cow's milk from a bottle. At maturity the two breed. Paredes had not heard the much repeated story (Maccagno 1932:56) that a lactating female alpaca can be induced to adopt a young vicuña by covering the latter with the skin of an infant alpaca, and that a vicuña, thus raised, will breed with alpacas. Belón used an alpaca as wet nurse for a vicuña, which later bred with an alpaca (Madueño 1912:16).

A paco-vicuña has a thicker neck and stouter legs than a vicuña, it weighs about twice as much, and it has wool about four times as long. Like vicuñas, these hybrids usually have a long bib of hair at the brisket. In 1952 Paredes had several "three-quarters" vicuñas produced by crossing a female paco-vicuña with a male vicuña. Inasmuch as a New York firm offered four-fifths of the price of pure vicuña wool

for the wool of these hybrids, there is promise that the production of paco-vicuña wool can be made a profitable business.

A program of work toward the perfection of paco-vicuña wool was strongly advocated 40 yrs ago by Madueño *(op. cit.)*. Provided that large quantities of uniform fiber are produced, paco-vicuña wool should be readily saleable. A satisfactory pure breed can probably be developed through selection and interbreeding, but this process is slow. A more rapid method of producing uniform paco-vicuña wool would be to cross individuals of a pure line of alpacas with pure vicuñas. This method would eliminate difficulties with inter-hybrid sterility and would produce, in one generation, many genetically similar hybrids that could be shorn. To eliminate difficulties caused by incompatability between parents that are members of different species, artificial insemination might be used. But for successful use of this method, a complete knowledge of the reproductive physiology of the alpaca and vicuña must first be obtained.

MANAGEMENT

Aside from the development of hybrid wool, how can the potential value of the vicuña best be realized by the countries of South America? Here are some suggestions for the increase, utilization, and development of the vicuña resource.

1. Enforce protective laws. Because of the lack of government agencies suited for the protection of wildlife, enforcement of wildlife laws is difficult. But existing police, army, and civil guard personnel could do much more than at present toward protecting vicuñas and setting a good example for others. Hunting from cars could easily be reduced. Prevention of the smuggling of hides and the illegal sale of vicuña articles would do much toward diminishing the slaughter of infant vicuñas. Restriction of this illegal trade would be aided by the enactment of a uniform set of protective laws in the four countries having vicuñas.

2. Restrain free-ranging dogs. Aside from men, dogs are the chief enemies of vicuñas. Dogs in the neighborhood of vicuñas should be restrained at night and kept near their masters by day. If it were official policy to shoot dogs that chased vicuñas, herdsmen might be more inclined to control their pets. A worthy effort would be to secure the cooperation of natives in keeping their dogs from chasing vicuñas, but among a dispersed native population such education is difficult.

3. Encourage vicuña ranching. Official encouragement, especially freedom from high export taxes, would make vicuña ranching attractive and perhaps profitable. However, as each vicuña may produce only $30 worth of wool before the end of its useful life, at about 10 yrs of age, even with large pastures and native labor at 25 cents a day it would seem unprofitable to raise vicuñas for an average return of only $3 per animal per year. Special inducements such as tax concessions are necessary. On the other hand, in many areas a small herd of vicuñas can be kept merely by protecting them from hunting. Vicuñas now receive this protection on some haciendas in Peru and Bolivia.

4. Harvest wild vicuñas methodically. As males greatly exceed the apparent number necessary for reproduction, a large number of them could be harvested periodically without diminishing the productivity of the vicuña population. If principally troop males were taken, disruption of vicuña society would be minimal. Hunting could best be done by a trained group, government or private, for untrained hunters could not be relied upon to distinguish between the sexes and age classes, to avoid crippling animals, and to make accurate reports of their kill. In certain favorable areas wild vicuñas might be captured by a modernized "chaco" system, sheared, and released. For any method of harvest the number of animals taken from any area each year should be based on the relation between population composition and density and the carrying capacity of the range. But determination of these factors requires continuous research and experimentation. Obviously supervision by men experienced in big game management practice is necessary to the wise utilization of the wild vicuña resource. The vicuña has survived centuries of persecution and abuse. It should respond in ideal manner to a sound management program.

SUMMARY

1. A study was made of the vicuña in the highlands of southern Peru by means of prolonged observation of groups in the wild. Most observations were made in a study area of approximately 1000 acres near Huaylarco, halfway between the cities of Arequipa and Puno. The main period of study was from May, 1951, to May, 1952.

2. Vicuñas inhabit semi-arid rolling grasslands and barren-appearing plains of the central Andes. They occur over a distance of about 1300 miles between the elevations of 12000 and 16000 ft, mostly above the 14000-ft level.

3. Of the senses of vicuñas, the best developed is sight. Hearing is but moderately acute, and the sense of smell is evidently poor. No observations indicated that other vicuñas, man, or carnivores were scented at a distance.

4. During daylight vicuñas alternately rest, lying prone, and graze, feeding chiefly on low perennial bunch grasses.

5. Social groups are of two major kinds: family bands, composed of an adult male accompanied by several females and young, and male troops, composed of many non-breeding males.

6. At Huaylarco the average band consisted of 1 male, 4 females, and 2 juveniles. The largest number of females observed in one band was 18, and the largest number of juveniles was 9.

7. The composition of a band usually remains constant for a period of several weeks. Most changes in composition are caused by the joining or departure of one or two females or immatures.

8. In normal movements the male leads his band.

In time of danger he warns the females with an alarm trill and interposes himself between the source of alarm and his females, as they retreat.

9. Each band inhabits, year around, a territory of from 20 to more than 100 acres in area. The group feeds, rests, and rears young in the territory.

10. The adult male defends the boundaries of his territory, whether he possesses females or not.

11. Defense is principally by means of aggressive action consisting of galloping to the territorial boundary and posturing erect, head and tail high. Pursuit and attempts to bite may follow.

12. Defense by the male is chiefly against other males, but females of transgressing bands are also attacked.

13. The male rarely takes action to prevent a female from leaving his territory. Yet, the females remain presumably because of familiarity with the home range and because of hostility toward them by members of surrounding bands.

14. The mutual boundary between two territories is apparently determined by the results of many encounters between the family males. Pendulum action results when an attacking male runs a short distance into his neighbor's territory and is then driven back.

15. Lack of territorial defense by the male, as when he is injured, results in dispersal of his females and loss of parts of his territory to neighboring males.

16. Territoriality as exhibited in the vicuña seems to be closely similar to the classical territory described for birds in that the males are spaced through pugnacity toward one another, that displays serve as a warning to other males, that the territorial boundaries rather than the females are defended, that a male is normally invincible in his own territory, and that males without territory constitute a reserve.

17. The apparent advantages of territorial behavior in the vicuña are protection of a feeding area, prevention of overstocking of the range, and reduction of strife.

18. Territorial size evidently depends on the food supply, for where forage is sparse and coarse territories are large, and where forage is abundant and succulent territories are small.

19. In the event that a band is driven from its territory, as by a man or dog, the group returns to the area within a period of several hours, even though the band members have been widely separated during the interim.

20. When a band has been driven far from its territory the male of the displaced band is relatively tolerant toward members of other displaced bands.

21. The male of a band is seldom hostile toward one or two females which join his group. Established females, however, are hostile toward those which join. During a period of a few days this hostility gradually ceases.

22. The juveniles of two neighboring bands may join and play together in both territories. Adult members of neither band are hostile toward the mixed group of young. In alarm these young retreat to their respective bands.

23. Young more than six months of age are treated by older vicuñas in much the same manner as established band females.

24. Young of both sexes leave bands at the time that new young are born, or a few weeks earlier. Departing yearling females join territorial males, while yearling males join male troops.

25. Male troops are leaderless aggregations consisting principally of yearling vicuñas.

26. At Huaylarco yearlings commenced to join troops in November. Yearling and two-year-old vicuñas constituted approximately nine-tenths of the membership of troops.

27. The troop is an open society, for the members join and leave freely. The members are kept together, somewhat loosely, by gregariousness and mutual tolerance.

28. The number of vicuñas in a troop may change several times a day. Many troops contain more than 30 males, and one troop of 75 was seen.

29. The range of movement of a troop depends on the distribution of forage, and on the frequency and persistence of attacks by territorial males. During a period of four days one troop moved a distance of more than 10 miles, though it remained within an area of two square miles.

30. At Huaylarco copulation was observed during March, April, and May. Most young were born during the first half of March, the first infant appearing on February 11.

31. During one observed birth a period of 15 minutes elapsed between the time of the first visible labor contractions and the dropping of the infant. The afterbirth fell an hour later. Observations indicated that the afterbirth is not eaten by vicuñas.

32. Approximately 15 minutes after being born the infant can stand, a half hour after birth it can walk, and at one hour of age it can run.

33. During daylight juveniles more than a week old rest, graze, and play together rather than with older vicuñas.

34. Until they are at least 8 months of age young sleep by their mothers. Until they are at least 10 months old they nurse several times a day.

35. Infant mortality is apparently high. At Huaylarco the ratio of juveniles to mature females at the end of the season of birth was 46 to 100.

36. The principal carnivorous enemies of vicuñas, especially juveniles, are Indian dogs. A group of 14 Andean condors was observed to attack a newborn vicuña, unsuccessfully. Andean foxes are numerous, and possibly important enemies of vicuñas.

37. On the basis of one animal per 50 acres of vicuña range, there are approximately one-quarter million vicuñas in Peru. This number is estimated to be more than one half of the total population.

38. On the best sites the average population density of vicuñas in bands, exclusive of juveniles, is about one animal per 10 acres. This rate of stocking

approximates the grazing capacity of the range.

39. Vicuñas may be temporarily displaced from their feeding grounds by alpacas, llamas, or sheep. Livestock consumes much forage that would otherwise be available to vicuñas.

40. Legal protection of vicuñas has been ineffective because of lack of law enforcement.

41. The vicuña population would probably respond well to wildlife management practices and could produce a large annual harvest of young males for meat and exquisite wool.

APPENDIX

DISTRIBUTION

Limits of present range.—Vicuñas are common in some undisturbed areas near the northern end of their range (Fig. 3), in the department of Junín, Peru, despite generally heavy use of the land. Rich mines have operated in that region for more than a century. I did not visit Junín, but Dr. D. F. Watson, of the Cerro de Pasco Corporation, wrote me (1954) that there are a "fair number" of vicuñas on ten haciendas in the region of the towns of Junín and La Oroya. Some occur as far north as the vicinity of Cerro de Pasco (now in the department of Pasco). In sections of Huancavelica, the department south of Junín, vicuñas are still common. This I judge from the reports of travelers who have driven over the cordillera in that region.

As to the southern extremity of the range, Romero (1927:132) states that Holmberg wrote, in 1901, that vicuñas ranged south to the border between the provinces of La Rioja and San Juan, Argentina. On the basis of the reports of other naturalists, Dr. Jorge A. Crespo, of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," thinks that the vicuña still occurs in San Juan (letter, 1954). Crespo also writes that the vicuña is well known in western Catamarca, near the Chilean border. In Chile too the range of the vicuña extends southward to about the latitude of northern San Juan (Argentina). Groups of as many as 60 vicuñas have been seen in the mountains east of the town of Vallenar, province of Atacama, Chile, by William R. Millie (verbal, 1953), a prominent rancher and keen naturalist of that area. But about 50 miles farther south, in the northern part of the province of Coquimbo, there seem to be no vicuñas, nor have there been any during the past few decades. These facts I judge from the experience of Rudolfo Wagenecht (verbal, 1953) of La Serena, an enthusiastic collector who has explored the cordillera of that region for many years.

In Bolivia vicuñas range eastward to the vicinity of Potosí and Cochabamba in Bolivia and, according to Dr. Crespo, in Argentina they range eastward to the Cordillera de Santa Victoria (longitude 65° W) in Argentina. In extreme southern Bolivia and in the southern parts of its range in Argentina, the eastern boundary of the distribution of the vicuña is poorly known (Fig. 3, dashed outline). Probably much of that region is too salty or arid to sustain forage for vicuñas. Nevertheless, Crespo reports them as abundant in parts of Jujuy, and common in western Salta (= central Los Andes). (Several Argentinian references mention vicuñas in the territory or "gobernación" of Los Andes, shown in figure 3. In 1944 that territory was apportioned among the provinces of Jujuy, Salta, and Catamarca.)

Former range.—How far north did vicuñas range in historical times? In his factual account of travels in the region of the Inca empire in the mid-sixteenth century, Cieza de León (Markham's ed. 1864:163), states that there were "scarcely any left" near Riobamba, Ecuador, that (p. 207) "there are . . . vicuñas" in the region of Loja, Ecuador and that (p. 288) "before the Spaniards arrived there were" vicuñas near Huamachuco, Peru (near latitude 8° S.). These records are inconclusive for they seem to be based on hearsay. The account of Tschudi (1847:314-315), written a century ago, tells of hunting vicuñas near Huayhuay (probably Huayllay, near latitude 11° S), Peru, and of having a pet at Tarma. These localities are no farther north than recent localities of record.

As to the southern end of the range, Molina's original description (1782) states that vicuñas were common in the mountains of Coquimbo, Chile, but this statement too lacks verification (Osgood 1943:233). Therefore, it appears that in historical times no great shrinkage of the range of the vicuña is adequately documented.

Many thousands of years ago, however, vicuñas apparently were not confined to the highlands, for portions of fossil skulls have been identified from Pleistocene and early Recent deposits in the region of the low pampas near Buenos Aires (López Aranguren, 1930:120). To explain the former occurrence in the lowlands of an animal that is now confined to a zone two miles higher in elevation, Cabrera & Yepes (1940: 268) suggest that either climatic conditions of the low pampas have changed greatly, or that a local form of vicuña was adapted to life there.

Altitude of occurrence.—In my travels I carried an aircraft altimeter and frequently checked the instrument readings at points of surveyed elevation. I found that some printed accounts give elevations 1000-2000 ft higher than is justified. No vicuñas were seen grazing on pastures higher than 16,000 ft. As to the lower limit of altitudinal distribution in Peru, I saw groups of a few vicuñas at sites as low as 13,000 ft near Mazocruz and Crucero, but there, as elsewhere in the vicinity of haciendas, it was possible that the animals seen may have been partly domesticated. While descending the road leading westward to Púquio, in the department of Ayacucho, in May of 1952, I saw bands of vicuñas at elevations as low as 12,400 ft. In Bolivia, men of the Rockefeller Foundation have seen many vicuñas near Lake Poopó and the town of Oruro, at elevations of about 12,100 ft (Dr. George Bevier, letter, 1953). Crespo (letter, 1954) reported vicuñas in numbers at 3800 m (about 12,500 ft) in northern Argentina. In Tarapacá, Chile,

carabineros living at Caritaya, 12,300 ft, told me that on occasions vicuñas approached their station. In general, then, the lower limit of occurrence of the vicuña is approximately 12,000 ft.

In the Andes, the elevation of biotic zones decreases as one goes southward, but vicuñas occur at no lower elevations in the southern part of their range than 20° of latitude farther to the north. Apparently they do not descend lower in the south because that region is relatively arid and suitable forage grows only above 12,000 ft.

Why are vicuñas limited to extremely high altitudes? Of course they must have physiological characteristics that allow them to live there. The blood of the vicuña, and of some other mammals native to high altitudes, is adapted to functioning with efficiency at low oxygen pressures (Hall 1937). Further, vicuñas have a wide tolerance for variations in atmospheric pressure. In zoological gardens near sea level vicuñas are healthy and they reproduce.

The principal factors that restrict vicuñas to high country are probably not physiological. Perhaps the species was formerly widespread, as suggested by fossils from the lowlands, and became extinct at lower levels where competition with other ungulates was severe. Inasmuch as change in elevation goes hand in hand with change in climate, vegetation, the numbers of humans and livestock, and other factors, critical evaluation of the influence of each factor on the distribution of vicuñas will not be possible until our knowledge of the ecology of the Andean highlands has been greatly advanced.

LITERATURE CITED

Allen, G. M. 1942. Extinct and vanishing mammals of the western hemisphere. Amer. Committee Internat. Wild Life Protection, Special Publ. **11**. xvi + 620 pp.

Acosta, J. (de) 1880. The natural and moral history of the Indies. Transl. E. Grimston. Ed. C. R. Markham. London: Hakluyt Society. **vol. 1.** xlviii + 295 pp.

Bowman, I. 1916. The Andes of southern Peru. Amer. Geographical Soc., N. Y. xi + 336 pp.

Burt, W. H. 1943. Territory and home range concepts as applied to mammals. Jour. Mamm. **24:** 346-352.

———. 1949. Territoriality. Jour Mamm. **30:** 25-27.

Cabrera, A. & J. Yepes. 1940. Mamíferos Sud-americanos. Buenos Aires: Compañia Argentina de Editores. 370 pp.

Cardozo, G. A. 1954. Los Auquénidos. La Paz, Bolivia: Editorial Centenario. 284 pp.

Carpenter, C. R. 1934. A field study of the behavior and social relations of howling monkeys. Compar. Psychol. Monog. **10:** 1-168.

Cieza de León, Pedro 1864: The travels of Pedro de Cieza de León, A. D. 1532-50, . . . Transl. and ed. by C. R. Markham. London: Hakluyt Society. xvi + lx + 438 pp.

Darling, F. F. 1937. A herd of red deer. London: Oxford Univ. Press. x + 215 pp.

———. 1952. Social behavior and survival. Auk **69:** 183-191.

Dice, L. R. 1952. Natural communities. Ann Arbor: Univ. Michigan Press. x + 547 pp.

Garcilaso de la Vega, Inca 1871. First part of the royal commentaries of the Yncas. Transl. and ed. by C. R. Markham. Vol. 2, 553 pp.

Gilmore, R. M. 1950. Fauna and ethnozoology of South America. **In** Handbook of South American Indians, Bull. 143, Smiths. Inst., Bureau Amer. Ethnology **6:** 345-264.

Hall, F. G. 1937. Adaptations of mammals to high altitudes. Jour. Mamm. **81:** 468-472.

Howell, A. B. 1944. Speed in animals. Chicago: Univ. chicago Press xii + 270 pp.

King, J. A. 1955. Social behavior, social organization, and poplation dynamics in a black-tailed prairiedog town in the Black Hills of South Dakota. Contrib. Lab. Vert. Biol., Univ. Mich., **67.** 128 pp.

López Aranguren, D. 1930. Camélidos fósiles Argentinos. Anales de la Sociedad Científica, Argentina **109:** 15-35, 97-126.

Maccagno, L. 1932. Los auquénidos peruanos. Lima: Dirección de Agricultura y Ganadería. 64 pp.

Madueño, C. G. 1912. Monografía de la vicuña. Santiago, Chile: Pan-Amer. Sci. Cong. **16**(2): 5-30.

Miller, G. S., Jr. 1924. A second instance of the development of rodent-like incisors in an artiodactyl. Proc. U. S. Natl. Mus. **66**, article 8. 4 pp.

Nice, M. M. 1941. The role of territory in bird life. Amer. Midland Nat. **26:** 441-487.

Osgood, W. H. 1943. The mammals of Chile. Field Mus. Nat. Hist., Chicago, Zool. Ser. **30.** 268 pp.

Pearson, O. P. 1951. Mammals in the highlands of southern Peru. Bull. Mus. Comp. Zool. **106:** 117-174.

Romero, E. C. 1927. Llamas y alpacas, vicuñas y guanacos. Buenos Aires. 208 pp.

Stroock, S. I. 1937. Vicuña. The world's finest fabric. New York: S. Stroock and Co., Inc. 23 pp.

Tinbergen, N. 1952. "Derived" activities; their causation, biological significance, origin, and emancipation during evolution. Quart. Rev. Biol. **27**(1): 1-32.

Tschudi, J. J. 1844-46. Untersuchungen über die fauna Peruana. St. Gallen. xxx + 262 pp.

———. 1847. Travels in Peru, during the years 1838-1842. Transl. T. Ross. London: David Bogue. xx + 506 pp.

Weberbauer, A. 1945. El mundo vegetal de los Andes Peruanos. Lima, Ministerio de Agricultura. xix + 776 pp.